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THE UNIVERSITY OF ALBERTA

HOME RANGE AND MOVEMENTS OF CLETHRIONOMYS GAPPERI IN THE NORTHERN BOREAL FOREST NEAR HEART LAKE, NORTHWEST TERRITORIES

by

(C) AUDREY BODNER WELLS

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE

OF MASTER OF SCIENCE

DEPARTMENT OF ZOOLOGY

EDMONTON, ALBERTA

FALL, 1976

THE UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled "Home Range and Movements of Clethrionomys gapperi in the Northern Boreal Forest Near Heart Lake, Northwest Territories," submitted by Audrey Bodner Wells in partial fulfillment of the requirements for the degree of Master of Science.

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Supervisor

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Date.....Oct 19/76.....

ABSTRACT

Movements and home range size of Clethrionomys gapperi were investigated during the summer of 1970 and the summer and fall of 1971 on a 13.75 ha plot near the Heart Lake Biological Station (60°51'N, 116°37'W), in the Northwest Territories. The CMR method was used, with live-traps placed on a 50.29 m grid and left in position for the entire trapping season. Data on all animals captured 5 or more times were used to draw home range maps and to establish home range sizes by use of standard measures: area (Minimum Polygon, Exclusive Boundary Strip), Observed Range Length (ORL), and Mean Intercapture Distance (MID).

Values for home ranges were larger than those recorded in the literature for Microtines, and in most cases several times larger than those recorded for C. gapperi. Male home range sizes were considerably larger than those of females, and males appeared to move about more.

Ranges overlapped considerably in both sexes and amount of overlap appeared to increase as the season progressed and numbers on the plot increased. Sex ratios never departed significantly from 1:1, and both sexes were captured with equal frequency, although males showed a tendency to use more traps as numbers of captures increased.

Seasonal differences in ORL's were observed for males but not for females. MID's also tended to be related to season, and did not appear to be affected by numbers on the plot.

Ranges of overwintered animals were larger than those of fall captured animals and ranges of those animals attaining sexual maturity early in the season were as large as those of overwintered adults. Fall range disintegration was accompanied by general unsettledness on the plot in both sexes, and density of animals in the fall was more than double the spring-summer density.

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INTRODUCTION

Home range is a concept that has been defined in many ways. The best known is Burt's (1943) definition: "that area traversed by the individual in its normal activities of food gathering, mating, and caring for young." Since 1943 much controversy has arisen and much work has been done in attempting to define home range parameters. Methods, especially those employed in attempting to estimate home range size, have come under close scrutiny.

Home range boundaries are ameboid and not static (Burt 1943) and are diffuse and general rather than sharply defined or outlined (Stickel 1954). In order to estimate the size or area of a home range, however, concrete boundaries must be assumed. Various workers (Hayne 1949, Stickel 1954, Brown 1956, Nikitina 1965) have collated the different methods of home range calculation, and have enumerated advantages and disadvantages for each. Some have made comparative studies using different methods for calculation of range areas (Mohr 1947, Stickel 1954, Mazurkiewicz 1971). Much has also been done regarding home range shape. Originally thought to be circular (Hayne 1949), they are now also assumed to be linear (Stumpf and Mohr 1962, Mohr 1965) or elliptical (Mazurkiewicz 1969).

A method for calculation of home ranges using a geometric center of activity was defined by Hayne (1949), and elaborated as standard diameters by Harrison (1958) and refined by Calhoun and Casby (1958). All of these methods necessitated circular home ranges and Jenrich and Turner (1969) and Mazurkiewicz (1969, 1971) modified and extended these methods to include elliptical home ranges using a bivariate normal distribution to allow for calculation of an elliptical area. The tendency for ranges to be elliptical was substantiated by Tanaka (1972) who also showed that

lengths of long and short axes of the elipse should not be calculated using the normal distribution. Recently, the validity of Hayne's (1949) center of activity concept has been tested (Smith, Boize, and Gentry 1973) with results indicating that animals were found in burrows on the outer edge of their known home ranges.

Hayne (1949) suggested that trapping mechanics caused a levelling off of calculated range area after a certain number of recaptures. According to various researchers, the number of captures required for reliable estimation of home range size differs since the curve for increase of range size per number of traps utilized levels off at different values, depending on range shape, type of area and other factors. Stickel (1954) used 10–12 captures as the minimum cut-off point; Mazurkiewicz (1971) 5 recaptures; Tanaka (1972) 6 or more recaptures. Metzgar and Sheldon (1974) developed a method by which it is possoble to compute an index of home range size that is independent of sample size and is free of assumptions regarding shape of home range and number of captures of each individual.

Distances between trapping points have also been reported to affect apparent size of home range. Closely spaced traps restrict animal's movements, while widely spaced traps make it difficult to establish boundaries precisely. Nikitina (1965) found that a 50 m grid was too large for Clethrionomys glareolus, while a 10–20 m grid spacing on a 5.8 ha plot was "ideal". Chitty (1937) found that widely spaced grid patterns favored linear captures of animals (C. glareolus). Mohr (1947), Hayne (1950) and Stickel (1954) found that calculated range area increased with increase of distance between traps. Davis (1953) suggested that traps be placed at varying distances from each other, but this complicated the analysis of data, and results obtained were usually the same as when a regular grid

pattern was used (Stickel 1954).

Nikitina (1965) suggested that range sizes are dependent upon distances between traps only when traps remain in position for a long time, and are not relocated during the course of the field work. The animals rely on the traps as refuges or feeding places. She also stated that traps could be left out for one week in forest situations, but this time was variable, depending on available food and shelter in the locality and population density. Burt (1943) in his definition of home range specifically excluded sallies from the normal range, but no completely objective method exists to differentiate exploratory sallies from the normal range travels (Tanaka 1972). Also, examination of an animal's movements for too long a time makes shifts from the normal range more noticeable.

The present study of red-backed vole, Clethrionomys gapperi in the northern boreal forest using a large trap grid on a large plot with a minimum amount of trap relocation is an attempt to:

1. Establish size of home range by standard measures; area, Observed Range Length (ORL), Mean Intercapture Distance (MID);
2. Determine whether home ranges are exclusive or whether they overlap;
3. Determine if differences in size of ranges exist in males and females;
4. Determine whether seasonal differences exist in home range sizes for both sexes;
5. Determine whether size of home range is influenced by population numbers; and
6. Determine whether home range sizes vary according to the ages of the individuals.

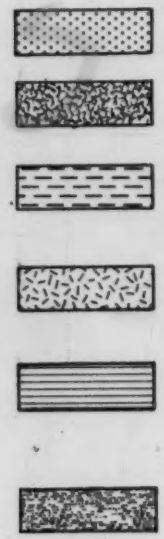
THE STUDY ANIMAL

C. gapperi prefers wooded areas and is reputed to prefer moist situations. Its diet is made up of a variety of plant and animal materials (Dyke 1971). Females are multiparous and have a gestation period of 17-19 days (Svihla 1929). Onset of breeding corresponds with spring thaw, and overwintered females within the study area may produce three litters a season (Fuller 1969). Females born early in the summer mature, but females born late in the summer remain immature (Fuller 1969). Overwintered males gain weight earlier than females in spring, suggesting an earlier onset in spring growth (Fuller, Stebbins, and Dyke 1969). In one study (Patric 1962), litter size and percentage of females breeding was inversely related to density. Young are weaned at about two or three weeks of age, and no voles are known to survive more than one winter.

THE STUDY AREA

Field work was carried out at the University of Alberta Research Station at Heart Lake, N.W.T., about 80 km (50 miles) west of Hay River. The 13.75 ha (34.38 acre) plot consisted of a rectangle 251.5 m x 553.3 m (110 rods by 50 rods), with its long axis lying approximately N - S magnetic (Fig 1). A low beach ridge that runs diagonally across the plot (included in the mixed white spruce - aspen association in Fig 1) is covered primarily by aspen (Populus tremuloides) and deciduous shrubs such as low bush cranberry (Viburnum edule), green alder (Alnus crispa), and prickly rose (Rosa acicularis). Jackpine (Pinus banksiana) stands are associated with an understory of juniper (Juniperus communis, J. horizontalis). Buffaloberry (Shepherdia canadensis) and shrubby cinquefoil (Potentilla fruticosa) are found in association with both P. banksiana and the less dense stands of white spruce (Picea glauca). Alnus crispa forms the major part of the

Figure 1. Plant associations on the study area



Dense white spruce with moss carpets

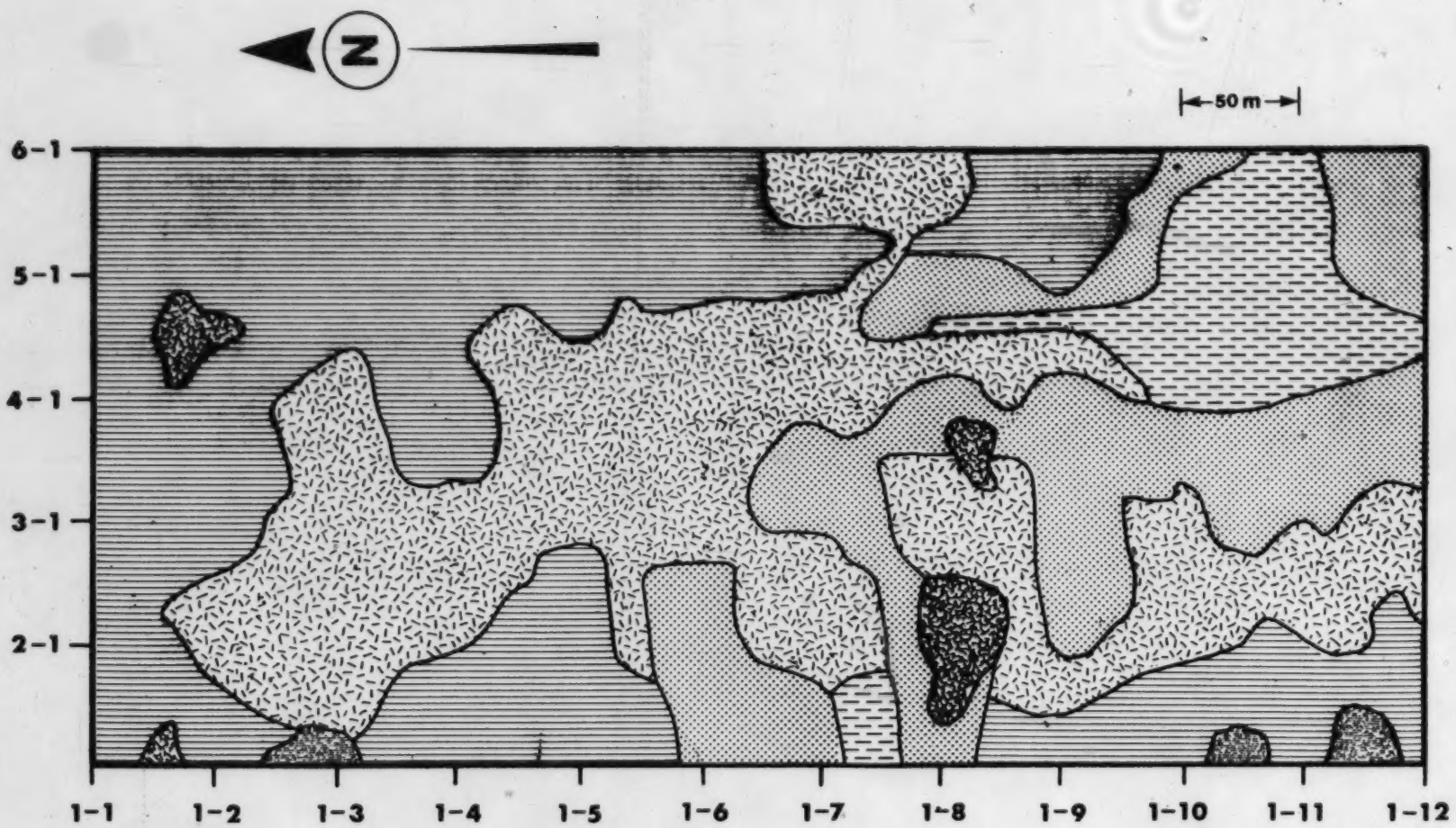
Thin white spruce with dense alder

Mixed white spruce, aspen, with well developed shrub layer

Mixed white spruce and jackpine, with well developed shrub layer

Park-like jackpine, scattered white spruce, buffaloberry and/or juniper and grass, and/or lichens

Open Juniper


N
50 m
6-1
5-1
4-1
3-1
2-1
1-1
1-2
1-3
1-4
1-5
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1-8
1-9
1-10
1-11
1-12

understory in less dense white spruce stands. No shrub layer occurs in dense white spruce areas which are found along the base of the beach ridge.

Ground cover is made up primarily of mosses and lichens, with large numbers of bog cranberry (Vaccinium vitis-idaea), bearberry (Arctostaphylos uva-ursi), wintergreens (Pyrola spp.) and bastard toadflax (Geocaulon lividum). Some aspen areas are characterized by presence of grasses (Elymus, Festuca, and Calamagrostis) and sedge (Carex sp.).

Area A has a higher proportion of open jackpine with little cover and was qualitatively judged to be inferior to Area B in habitat.

Clethrionomys shares the study plot with deer mice (Peromyscus maniculatus), meadow voles (Microtus pennsylvanicus), and heather voles (Phenacomys intermedius). Shrews were not captured, but probably were present at very low density. Chipmunks (Eutamias minimus) were present and were occasionally captured. Potential predators were weasels (Mustela erminea) and marten (Martes americana). Canada jays (Perisoreus canadensis) attacked animals released from traps, and a red fox (Vulpes vulpes) with mange, attracted by a garbage pit and litter left near a public area, frequented the plot. No account was kept of raptorial birds.

MATERIALS AND METHODS

Grid lines at 50.29 m (10 rod) intervals divided the plot into six parallel lines of 12 trapping stations. Three Longworth traps provided with lab chow, sunflower seeds and terylene batting were placed within 3 m (10 ft) of each stake marking an intersection of grid lines. During the first season (1970), traps were left in position the entire season, concealed under logs or other natural cover, and protected from direct insolation wherever necessary by pads of sphagnum or lichens. Traps were only open on one half of the plot at any given time, the north (A) and

south (B) halves being trapped for seven consecutive days in alternate weeks. Each such trapping period is referred to as a Rota. Nest boxes were cleaned and contents replenished, and tension of the release mechanism was checked at the beginning of each trapping period and at the time of release of each captured animal. Traps were inspected twice daily in mild weather, and three times daily on hot-dry or cool-wet days. Frequent walking of the grid during trap checks resulted in formation of trails.

Trapping procedures remained relatively unchanged the second field season (1971) with alternate halves of the plot being trapped alternate weeks, but in addition, in order to try to further delineate or define range boundaries, traps in selected areas were rotated every two days to locations half-way between trap points. Also, for one week, the two sub-plots were run synchronously.

The trapping season was begun on May 13 in 1970, and continued until August 27. The season was started later in 1971, on May 17, because of a late spring snowfall, and carried through until August 23, when traps were picked up for a 2 - week interval. The traps were washed, rebaited and reset from September 9 until October 7 when freezing rains and frosts lowered trap efficiency and caused deaths due to exposure.

All animals that succumbed in the traps due either to overheating or cooling were autopsied, and skulls were kept for age determination. In the fall of the second field season (1971), area B was snap-trapped with two Museum Special traps per station on rows and midway between them (a distance of 25.15 m). The following spring the entire plot was snap-trapped again, this time with two additional points, making a 12.57 m grid. Animals that were snap-trapped from October 10-15 on area B and in the spring of 1972 on the entire plot (A and B) were also autopsied and their

skulls and internal parasites were saved.

Animals were initially marked by toe-clipping, later by both toe-clipping and ear-tagging. In addition, they were weighed to the nearest 0.5 g using a Pesola spring balance equipped with a clip that in turn was attached to the nape of the animal's neck. Thus suspended it could not struggle much, facilitating fast, accurate reading of the scale. Position of testes in males and presence or absence of vaginal mucous plugs in females were also noted.

The data for the home range size (either linear or area) include animals that were captured on the boundaries of the plot, as long as these animals were captured at least five times. (See graphs of captures vs. number of trap points in Results.) Exploratory trips were excluded whenever they were detected.

Home ranges were calculated using several techniques: Observed Range Length (ORL), Mean Intercapture Distance (MID), Minimum Polygon technique, and Exclusive Boundary Strip. All of these are described and discussed by Hayne (1949) and Stickel (1954) who also enumerated advantages and disadvantages of each method.

In calculating home range length or area, zero values occurred in both male and female groups when an animal had been captured repeatedly at only one point. Since a zero value is not possible unless the animal was sedentary, a value of 50 m was given to each zero value individual in calculations of Observed Range Length (ORL). The distance of 50 m was chosen because it was half the distance to the next trapping point, taken on each side of the trap point. This procedure was also used when home range areas were calculated.

RESULTS

Demography

Numbers

During this study, 469 animals of four different species were captured and marked (Table 1), 154 in 1970, 315 in 1971. The results and discussion will be centered on C. gapperi (402 animals). For all other species, insufficient data are available to plot reasonably accurate home ranges. P. maniculatus was the second most abundant species, but most individuals were taken in border traps, thus making any calculations of home range suspect. P. intermedius and M. pennyslvanicus were not common in the region.

The numbers of C. gapperi and P. maniculatus combined were remarkably similar for the period from May to August in each year (Table 1). A decline in C. gapperi in 1971 was compensated by an increase in P. maniculatus.

In September and October of 1971, however there was an influx of unmarked C. gapperi onto the plot which resulted in a doubling of the population marked for the season. Whether this doubling, or at least an increase in numbers also occurred the previous year could not be confirmed in this study since the trap season ended in August of 1970.

C. gapperi were about evenly distributed on the two halves of the plot with area B harboring a slight excess of animals in the summer trap season of 1970, and a greater excess in the fall season of 1971 (Table 2). In the summer of 1971, area A harbored more animals.

Numbers of individuals captured per day were extremely variable when taken in 2 - week periods throughout the season. Numbers remained relatively stable in 1970 (7 ± 2) with only very gentle peaks (Fig 2A). The lowest level occurred in time period III, from June 8–21 (Table 3). In the spring

Table 1. Total numbers of 4 species of animals captured in live-traps on the study grid, including those that died in traps and those captured only once.

	1970	1971		1971 (Total)
	13 V-27 VIII	17 V-23 VIII	9 IX-15 X	17 V-15 X
C. gapperi	135	109	158	267
P. maniculatus	17	46	1	47
M. pennsylvanicus	2			
P. intermedius		1		1
Total	154	156	159	315

Table 2. Numbers and sex ratios of C. gapperi during major trapping periods on the study grid.

	Live-trapped									Snap-trapped					
	1970			1971						1971			1972		
	May 13–Aug 27			May 17–Aug 23			Sept 9–Oct 7			Oct 10–15			May		
	n	χ^2	%♂	n	χ^2	%♂	n	χ^2	%♂	n	χ^2	%♂	n	χ^2	%♂
Area A	65	.121	46	61	.074	52	67	3.69	34	*			16	2.00	75
Area B	70	.126	53	48	.153	54	91	.373	46	62	.516	58	22	.818	64
Total	135		50	109	.164	53	158	1.92	43				38	2.58	68

* not trapped

and summer season of 1971, values again closely resembled those for 1970, although they were slightly higher (9±4). Again, the lowest value occurred in time period III, form June 14-27. However, while values at the end of the season were beginning to decline in 1970, in 1971, when trapping was stopped during time period VII, August 9-15, mean numbers of individuals captured had increased to double that of the low during time period III. When trapping continued in September, (time period VIII) numbers continued to rise until at the end of the fall season (time period IX) they were double the number that had been captured at the end of the summer season (time period VII). In the fall increase in numbers of individuals, mean daily captures of males and females were almost equal (Fig 2, B and C) although in actual numbers more females were captured than males during this period (Fig 3).

Rises in numbers of individuals captured daily roughly correspond with emergence of juveniles, which began in time period IV in both seasons.

Although the young began to appear in time period IV in both years, numbers of unmarked animals did not start increasing until time period V in 1970. Then throughout the season and until its end, in each time period a slight majority of unmarked individuals were females (Fig 3).

In 1971, an increase in unmarked individuals began in time period IV but numbers of unmarked animals were not definitely in favor of females until the fall trap season, when more of the newly captured animals were females.

In 1970, mean daily capture of males was on the average lower than that in 1971, while mean daily captures of females were slightly higher in 1970 than 1971 (Fig 2, B and C). The fall values in both males and females are more than double the spring-summer captures.

Table 3. Relationship between time periods as used in the text, trapping rota , and calendar dates.

	ROTA	TIME PERIOD	DATE
1970	1&2	I	May 13-24
	3&4	II	May 25-June 7
	5&6	III	June 8-June 21
	7&8	IV	June 22-July 5
	9&10	V	July 6-July 19
	11&12	VI	July 20-August 2
	13&14	VII	August 3-August 16
	15&16	VIII	August 16-August 27
1971	1&2	I	May 17-30
	3&4	II	May 31-June 13
	5&6	III	June 14-June 27
	7&8	IV	June 28-July 11
	9&10	V	July 12-July 25
	11&12	VI	July 26-August 1
	13	VII	August 9-15
	15&16	VIII	September 9-September 23
	17&18	IX	September 24-October 7

Figure 2. Mean numbers of C. gapperi captured daily, taken at 2 - week intervals. Horizontal lines are means; boxes show 95% confidence intervals; and vertical lines indicate ranges. Total number of animals caught during the 2 - week period is indicated in parantheses. Fig 2A represents number of males and females; Fig 2B represents numbers of males only; Fig 2C represents numbers of females only.

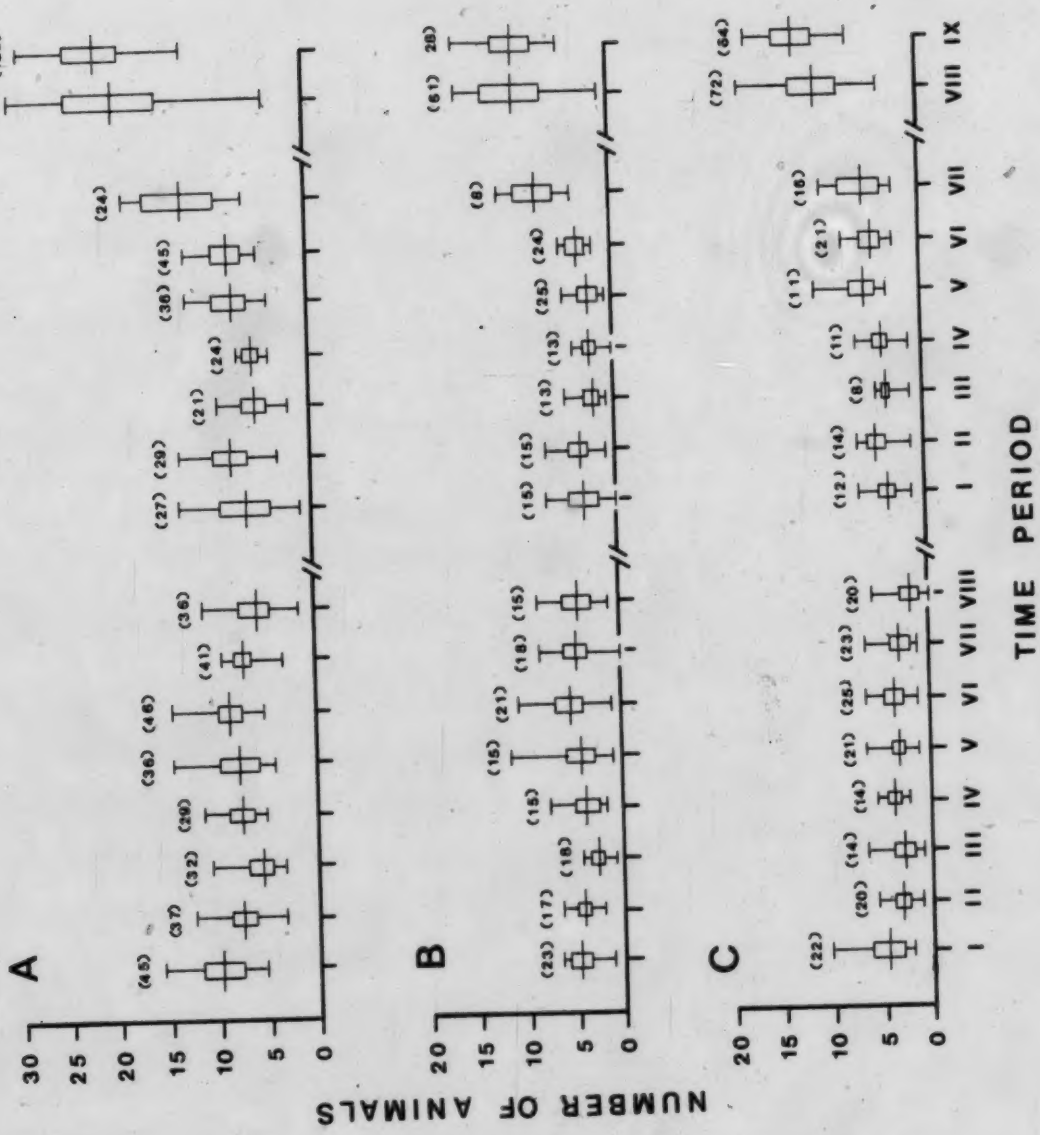
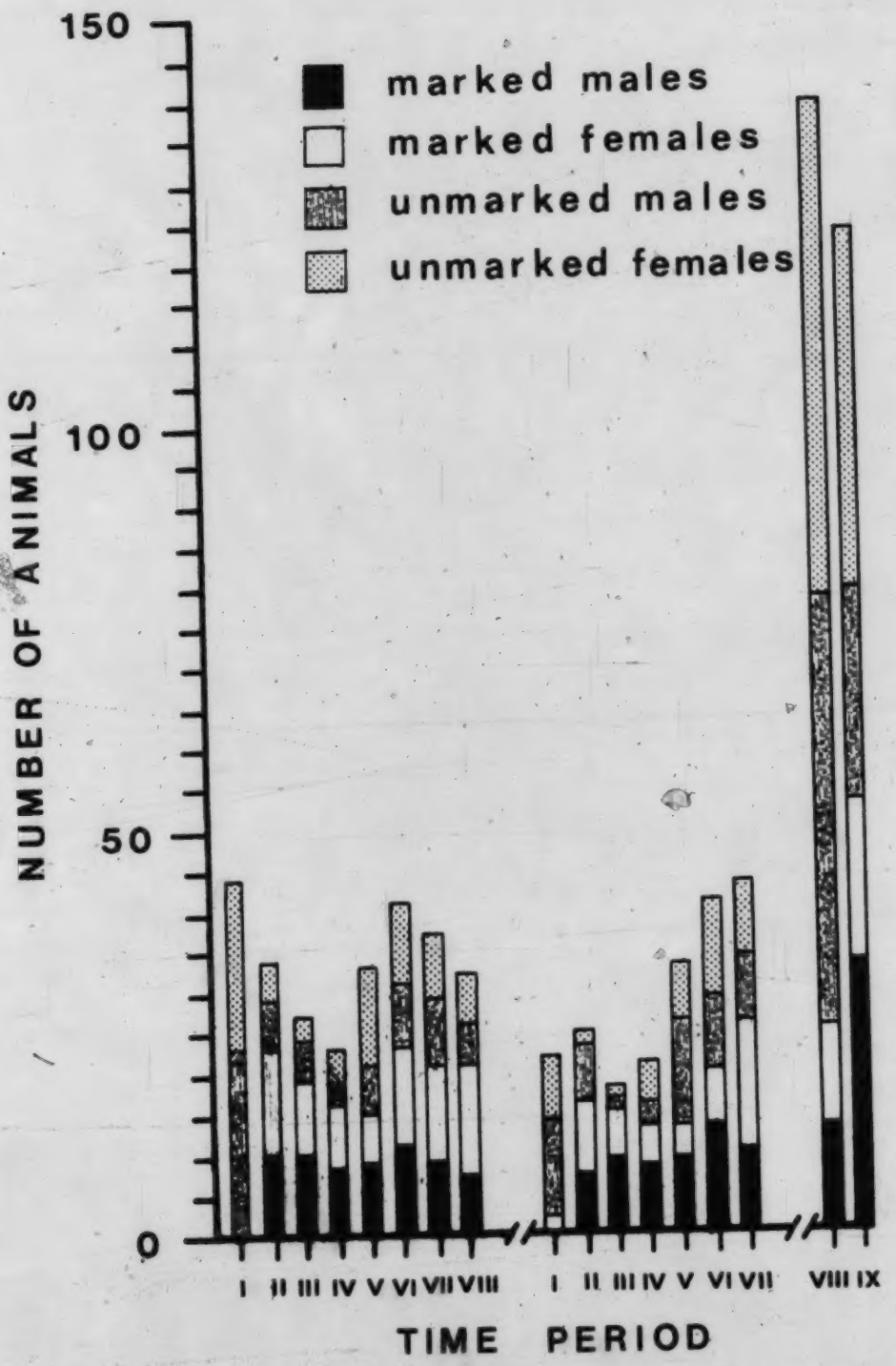

A
B
C
NUMBER OF ANIMALS
TIME PERIOD
I II III IV V VI VII VIII
I II III IV V VI VII VIII IX

Figure 3. Total number of marked and unmarked male and female C. gapperi during each time period in 1970 and 1971.


150
100
50
0
NUMBER OF ANIMALS
marked males
marked females
unmarked males
unmarked females
I II III IV V VI VII VIII I II III IV V VI VII VIII IX
TIME PERIOD

Sex Ratios

On area B, the sex ratio never departed significantly from 1:1 either in 1970, 1971 or 1972 when the plot was snap-trapped (Table 2) although fluctuations occurred in total number of animals captured. On area A, total numbers of animals captured remained relatively constant. Throughout the entire spring and summer seasons of 1970 and 1971, males made up 46 and 52% of the population, respectively. However, in the fall (September 9 - October 7) numbers of males had dropped to 34% of the trapped sample (χ^2 = 3.69; $p > 0.05$). When area A was snap-trapped in the spring, 75% of the sample were males (χ^2 = 2.00; $p > 0.05$). When results for areas A and B are combined, the ratio remains 1:1 in both 1970 and 1971. Snap-trapping indicated that although numbers of animals were lower in the spring, percentage of males in the population had increased, though not significantly (Table 4).

Survival

Winter More animals had survived the winter of 1969-70 than 1970-71 although the number of animals that entered that winter (1969-70) is unknown. Of a possible 35 animals known to be alive in the fall of 1970, (Fig 3) only 2 marked animals (both females) were recaptured in a sample of 22 taken in the spring of 1971. Of the 73 marked animals that entered the winter of 1971-72 (Table 5), 12 were recovered in the spring of 1972 (Table 4), with the largest proportion being August-marked animals (Table 5). This number might have been larger if the B half of the plot had not been snap-trapped in the fall of 1971. This larger sample of marked animals in 1972 may indicate that trapping was ended too early in the fall of 1970 and that a great deal of mixing may be caused by this general fall unsettledness.

Table 4. Numbers and sex ratios of marked and unmarked snap-trapped *C. gapperi*.

	FALL 1971						SPRING 1972					
	Unmarked			Marked			Unmarked			Marked		
	n	χ^2	%♂	n	χ^2	%♂	n	χ^2	%♂	n	χ^2	%♂
Area A	*						8	.25	63	8	2.25	88
Area B	24		50	38	.842	61	18	.44	61	4	.5	75
TOTALS	24		50	38	.842	61	26	.69	62	12	.66	83

* not snap-trapped

Table 5. Proportions of C. gapperi surviving during the trapping seasons of 1970 and 1971, and winters of 1970-71, 1971-72.

Year	Month Marked	Number Caught	Proportion Unmarked	Proportion Surviving Until the End Of: May	June	July	August	September	October	May	June
1970	May	52	1.000	.385	.154	.058	.038			.000	.000
	June	35	.429		.400	.200	.200			.000	.000
	July	53	.763			.462	.282			.000	.000
	August	53	.547				.552			.069	.069
1971	May	22	.909	.750	.250	.150	.000				
	June	30	.433		.615	.385	.077	.000			
	July	54	.759			.658	.316	.000			
	August	68	.485				.485	.485	.121	.091	
	September	168	.821					.333	.203	.058	
	October	73	.274						.950	.050	
1972	May	38	.684								

Even though area B was snap-trapped in 1971, more animals were snap-trapped on it in the spring of 1972 than on area A, which was left undisturbed in the fall of 1971 (Table 4). However, a larger proportion of area A animals were marked (50% as opposed to 18%).

Summer In both 1970 and 1971, by the end of August, May and June captured animals made up a very small proportion of the population (Table 5). Nearly half of the populations in both years were made up of August captures, and 1/3 of the populations of July captures. By October of 1971, May, June, and July captured animals had disappeared, and more than half of the population was made up of September captures.

Monthly survival of overwintered animals (Table 5) (i.e. May and June captured animals) appeared to be better in 1970 than in 1971, with a larger proportion making an appearance in the August sample. The proportion of animals initially caught in 1970 was much lower than that in 1971, although May to June and June to July survival was especially higher in 1970 than 1971. In both years, however more so in 1971, the worst survival of overwintered animals occurred from June to July and from July to August. Best monthly survival of young of the year occurred in the August caught sample.

Activity

When the number of animals captured per day was divided into those caught during the evening trap check (day active) and those captured during the morning trap check (night active) in both 1970 and 1971, number of captures was initially the same during the morning and evening trap checks (Fig 4), indicating no preference for nocturnal over diurnal activity. Near the end of July and beginning of August, larger numbers were caught in the morning than in the evening suggesting a tendency toward nocturnal

activity as nights lengthened. This separation was especially noticeable when trapping was resumed in September, 1971.

Home Range

Introduction

Two problems plague the student of home range as revealed by live-trapping. How many captures are necessary to give an adequate picture? How do you recognize exploratory sallies?

I attempted to answer the first question by plotting number of times an individual was captured against number of different traps used by that individual. Representative results are displayed in Figures 5 and 6. It is clear that females reach a plateau rather rapidly so that for them I felt justified in including all animals captured 5 or more times (4 or more recaptures). Some males (eg. G-164, G-37) behaved much like females, whereas others, notably G-152, and G-36 were still adding to their trap-revealed home ranges after 50 captures. In most cases in males, a small plateau occurred after 4-7 captures so I also used 5 captures as the cut-off point for males. On these bases, 44 animals caught in 1970 qualified plus 59 in spring-summer of 1971, and 34 in September-October of 1971 (Table 6).

On the second point, I drew maps of all trap-revealed ranges of all animals that qualified (Fig 7, 8, 9). Some exploratory trips were easy to identify (Fig 8, Fig 9A) whereas others were less obvious (Fig 7, Fig 9C). Final decision as to what to include in the home range was made subjectively. The movement in Fig 8 I classed as exploratory. The extreme movement in Fig 9A I also classed as exploratory in nature, while movements mapped in Fig 9C were accepted as due to normal activities.

All females captured 5 or more times in both years were captured at

Figure 4. Daytime (●) vs. night time (■) captures of C. gapperi by 2 - week intervals for the whole plot. Note the similarity in numbers captured around the solstice (Periods II - IV) and the separation as nights lengthen in August (Periods VI - IX)

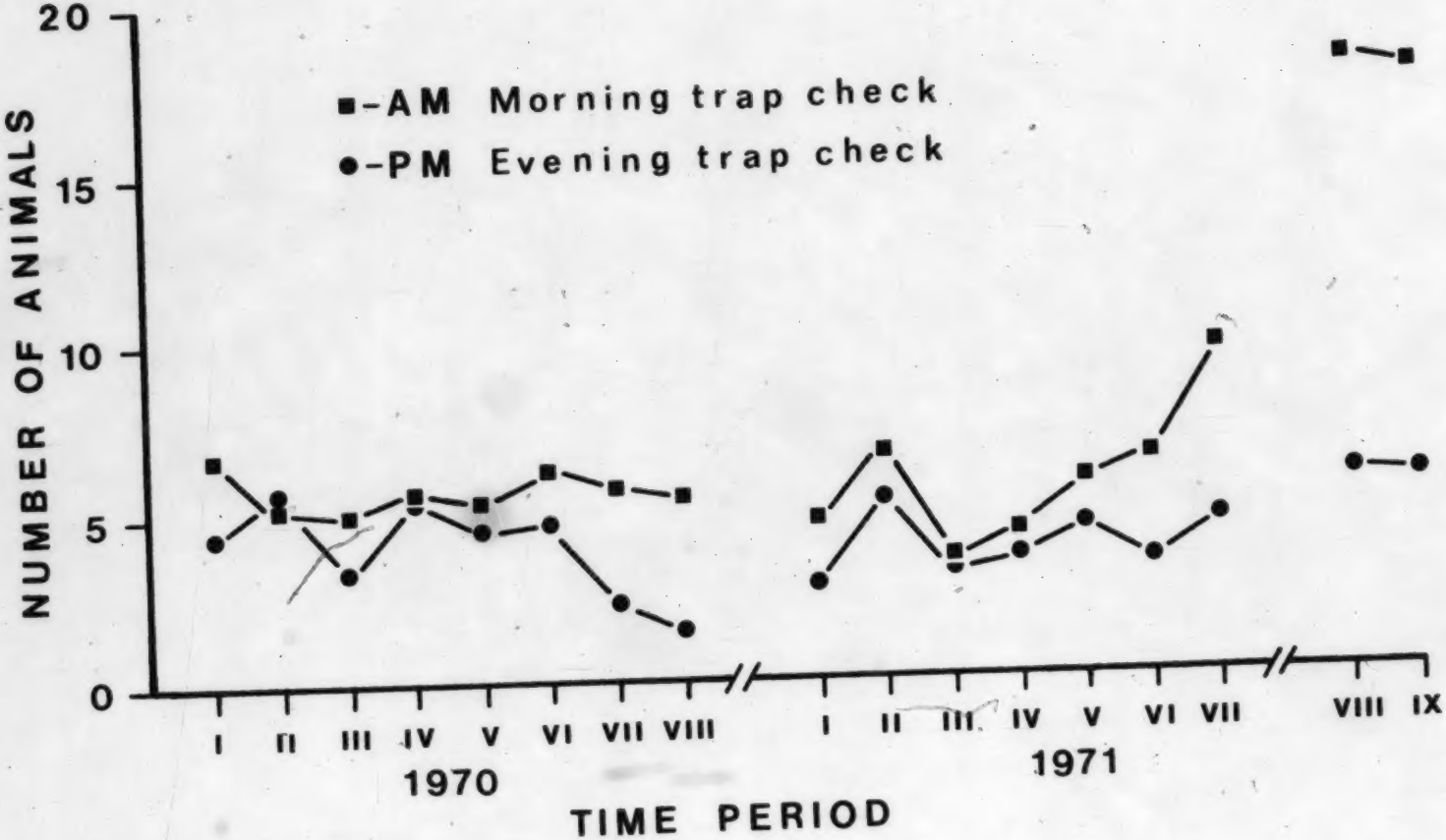

20
15
10
5
0
NUMBER OF ANIMALS
■-AM Morning trap check
●-PM Evening trap check
I II III IV V VI VII VIII
1970
I II III IV V VI VII VIII IX
1971
TIME PERIOD

Figure 5. Representative results of number of captures of individual C. gapperi plotted against number of traps the individual used, to determine how many captures are adequate to plot a home range. The y - axis represents number of trap points; x-axis the number of captures. 1970 females are represented on the left side of the page, 1971 females on the right. YOY stands for young of the year; OW for overwintered animals.

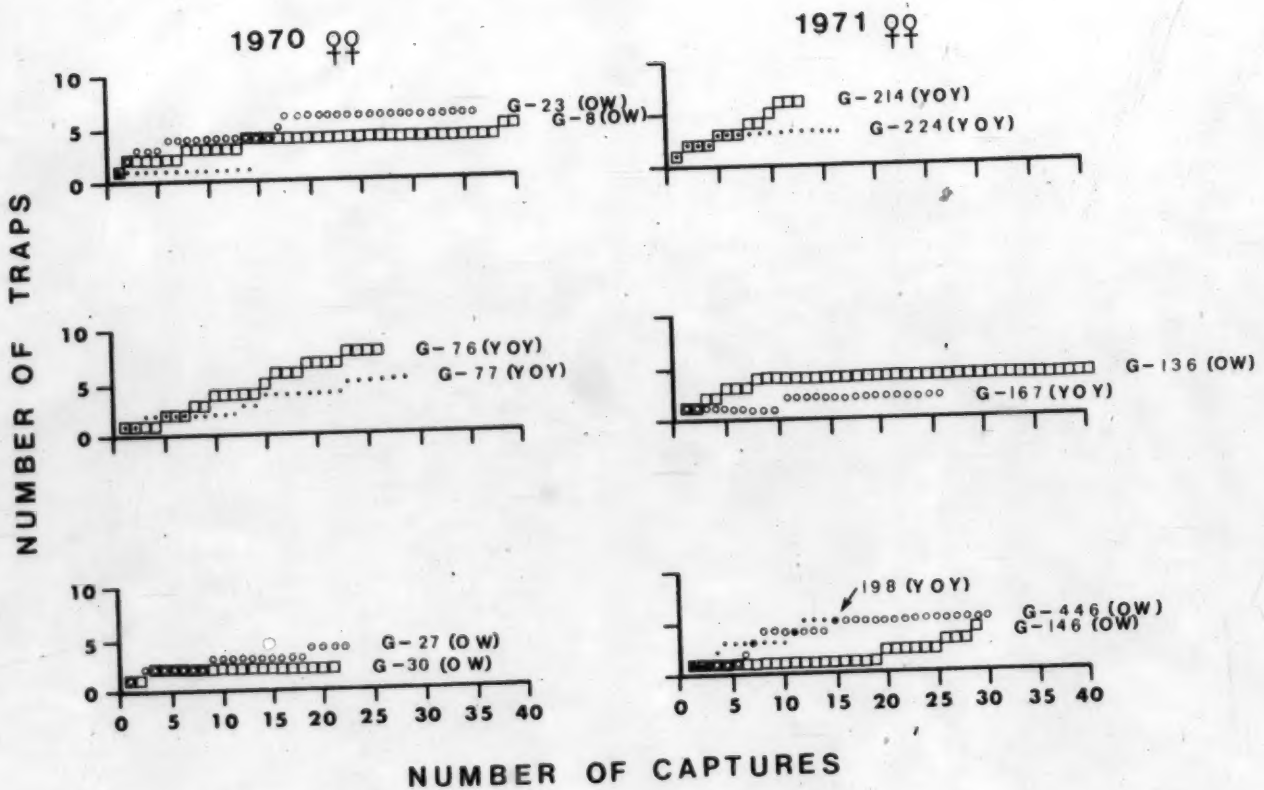

1970 ♀♀
1971 ♀♀
NUMBER OF TRAPS
NUMBER OF CAPTURES
G-23 (OW)
G-8 (OW)
G-214 (YOY)
G-224 (YOY)
G-76 (YOY)
G-77 (YOY)
G-136 (OW)
G-167 (YOY)
G-27 (OW)
G-30 (OW)
198 (YOY)
G-446 (OW)
G-146 (OW)
0
5
10
15
20
25
30
35
40

Figure 6. Representative results of number of captures of individual C. gapperi plotted against number of traps the individual used, to determine how many captures are adequate to plot a home range. The y-axis represents number of trap points; x-axis the number of captures. 1970 males are represented on the left side of the page; 1971 males on the right. YOY stands for young of the year; OW for overwintered animals.

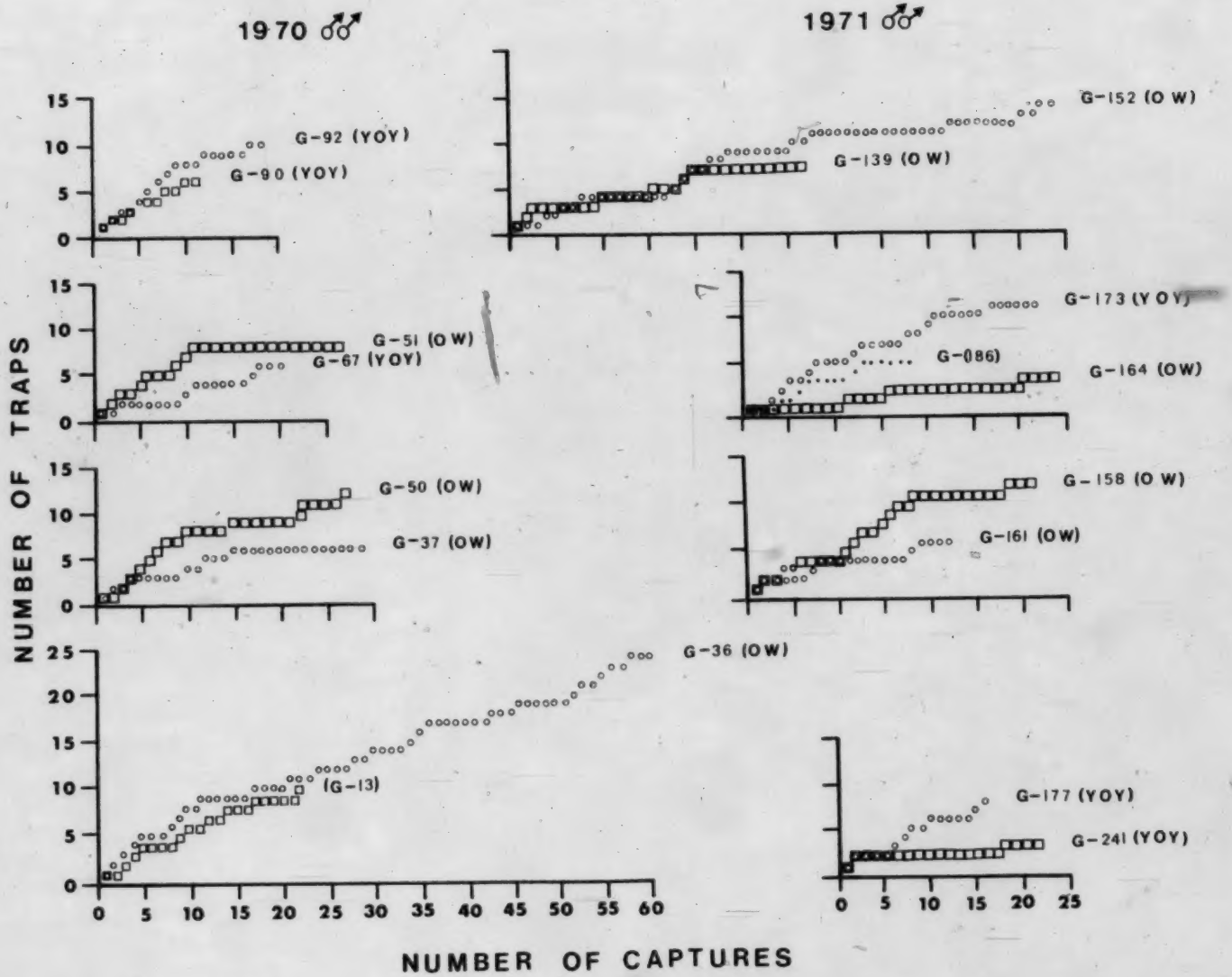

1970 ♂♂
1971 ♂♂
G-92 (YOY)
G-90 (YOY)
G-152 (O W)
G-139 (O W)
G-51 (O W)
G-67 (YOY)
G-173 (YOY)
G-086)
G-164 (OW)
G-50 (OW)
G-37 (OW)
G-158 (O W)
G-161 (OW)
G-36 (OW)
(G-13)
G-177 (YOY)
G-241 (YOY)
NUMBER OF TRAPS
NUMBER OF CAPTURES

Table 6. Breakdown of number of C. gapperi captured fewer than 5 and more than 5 times on the study grid in the summers of 1970 and 1971, and the fall of 1971.

		NUMBER OF CAPTURES																									
		<5	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21-25	26-30	31-35	36-40	41-45	46-50	>50	Total ≥5	Total Animals
1970 May to August	♂	49	1	2	2	1	3		1	1			1		1		1		2	2					1	19	68
	♀	42	1	2	2	3	2	1		2		1	1			1	1	1	1	2	2		1		1	25	67
	Total	90	2	4	4	4	5	1	1	3		1	2		1	1	2	1	3	4	2		1		2	44	135
1971 May to August	♂	26	3	4	4	3	2		1		1		1	1	1	3	1		2	0	4				1	32	58
	♀	24	2	3	1	3	2	3			3		1		2	1		1	1	3		1				27	51
	Total	50	5	7	5	6	4	3	1		4		2	1	3	4	1	1	3	5	2	1			1	59	109
1971 September to October	♂	47	5	4	2	2	1	2	2			2	1													21	68
	♀	77	4	3	2	1			1							2										13	90
	Total	124	9	7	4	3	1	2	3			2	1			2										34	158

Figure 7. Trap-revealed home range of G-36 male showing no obvious exploratory trips. Size of circles is proportional to frequency of capture at each station.

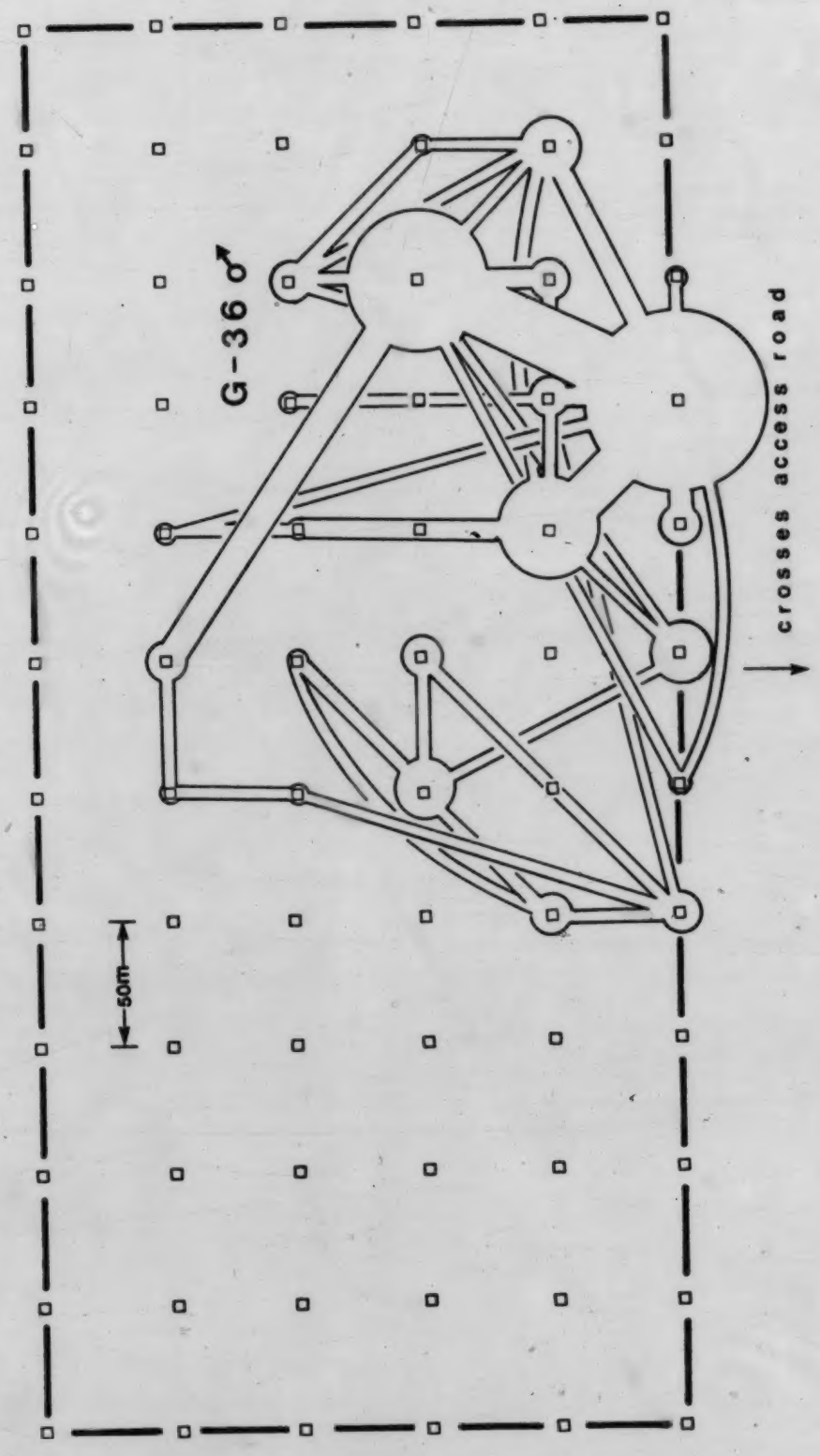

G-36 ♂
crosses access road
50m

Figure 8. Trap-revealed home range of G-158 male showing one obvious exploratory trip to station 3-4. Size of circles is proportional to frequency of captures at each station.

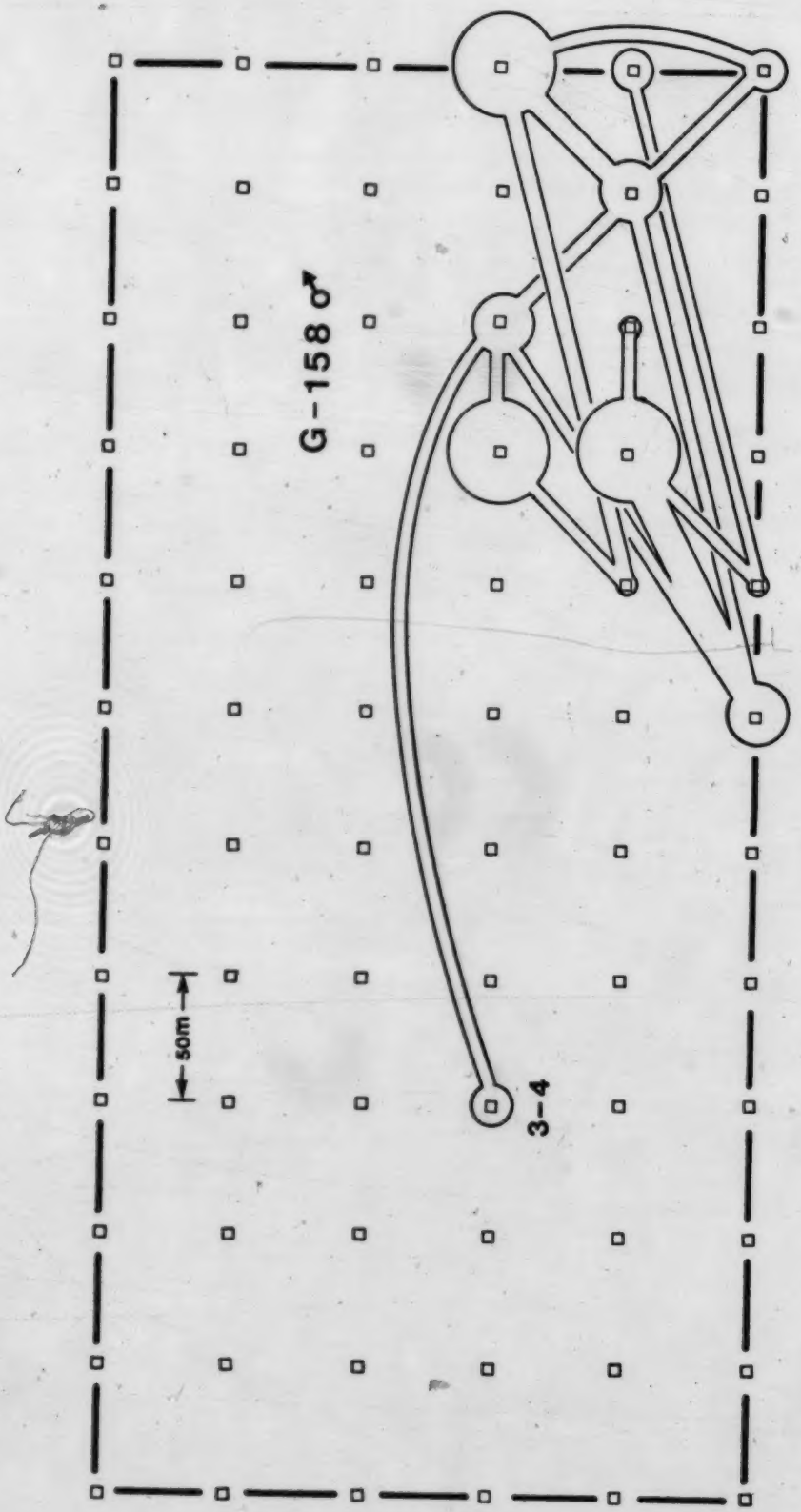
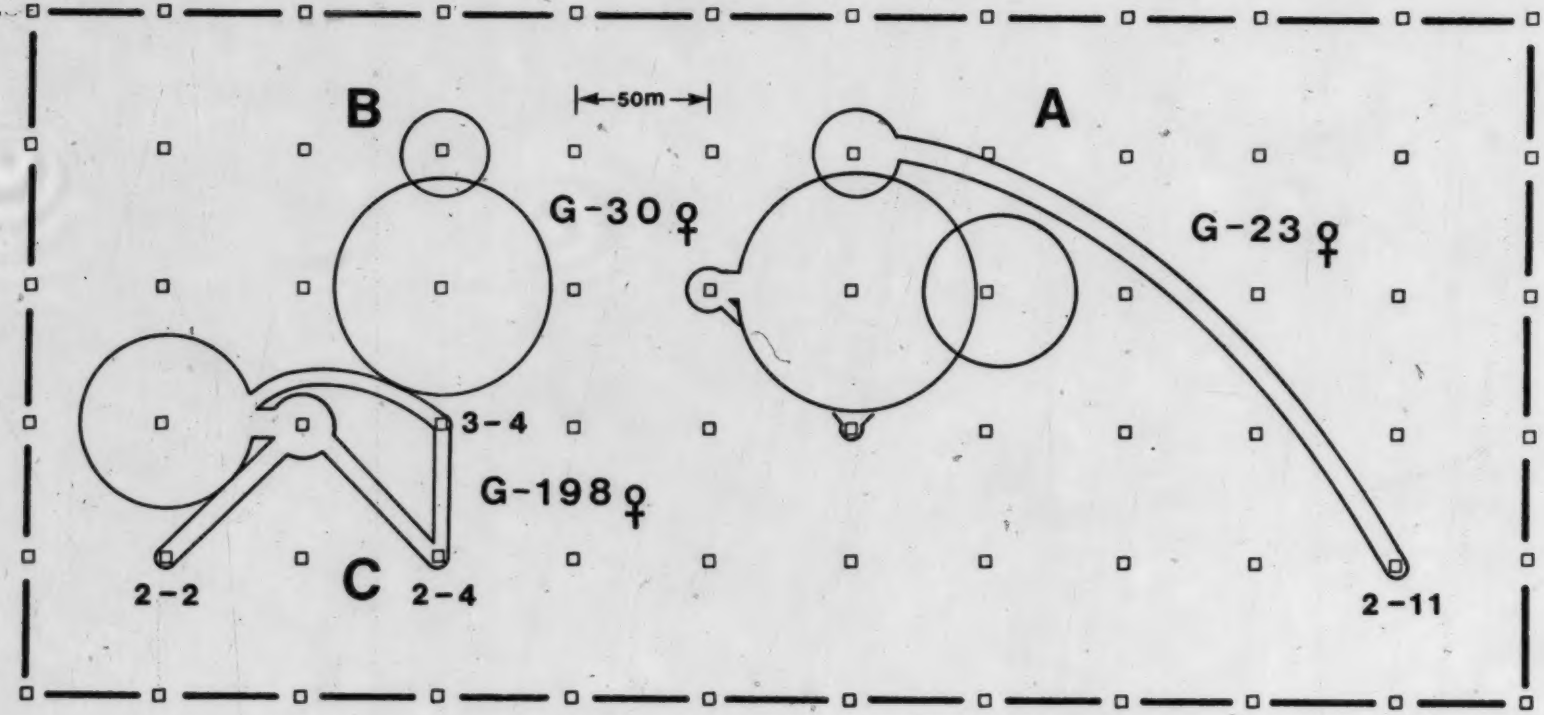

G-158 ♂
50m
3-4

Figure 9. Trap-revealed ranges of 3 female C. gapperi. Most female ranges resemble C (G-30), in lacking exploratory trips. A (G-23) shows one obvious exploratory movement to station 2-11. Size of circles is proportional to frequency of capture at each station. Difficulty arises in cases such as C (G-198), whose visits to 2-2, 2-4 and 3-4 could be considered as short exploratory trips. I decided, subjectively, however, not to consider them as such.


B
50m
A
G-30 ♀
G-23 ♀
3-4
G-198 ♀
2-2
C
2-4
2-11

1-9 different trap points on the plot, with 88% being captured at 2-5 points in 1970, and 80% being captured at 2-5 points in 1971 (Fig 10 B). In the female group, in 1970, one animal used 6 capture points in 8 captures, but in both years, although individuals were captured as many as 40 times in 1971, and 55 times in 1970, no female ever used more than 9 trap points. No substantial differences occurred between years in spite of the addition of traps at 25 m intervals late in the summer of 1971 (See Methods). In the females, therefore, there was no tendency to use more traps with increased number of captures after the first few recaptures.

Males were captured at 1-23 trap points in 1970, with 89% being captured at 2-10 trap points. In 1971, males were captured at 1-19 trap points with 92.5% of them being captured at 2-8 trap points (Fig 10 A). When the trap grid was altered in 1971, the revised spacing did not change the number of capture points significantly but did allow for more recaptures per individual. Males also showed a tendency to use more traps as the number of recaptures increased. Up to about 10 captures, males and females were similar (1-6 traps). Beyond 10 captures, males continued to use additional traps.

Male home ranges could usually not be drawn with confidence since few of the ranges were completely within the confines of the plot. The situation differed somewhat for females since they occupied fewer trap points and some of the females had their entire area of activity encompassed by plot boundaries. Many females, however, also had ranges that bordered on plot boundaries.

Observed Range Length (ORL)

Observed range length is the distance between the most widely separated capture sites and is a linear expression of home range size. Its

Figure 10. Number of captures and number of traps utilized by male (A) and female (B) C. gapperi, grouped in the following trapping periods:

● Spring-Summer 1970

○ Spring-Summer 1971

▲ Fall 1971

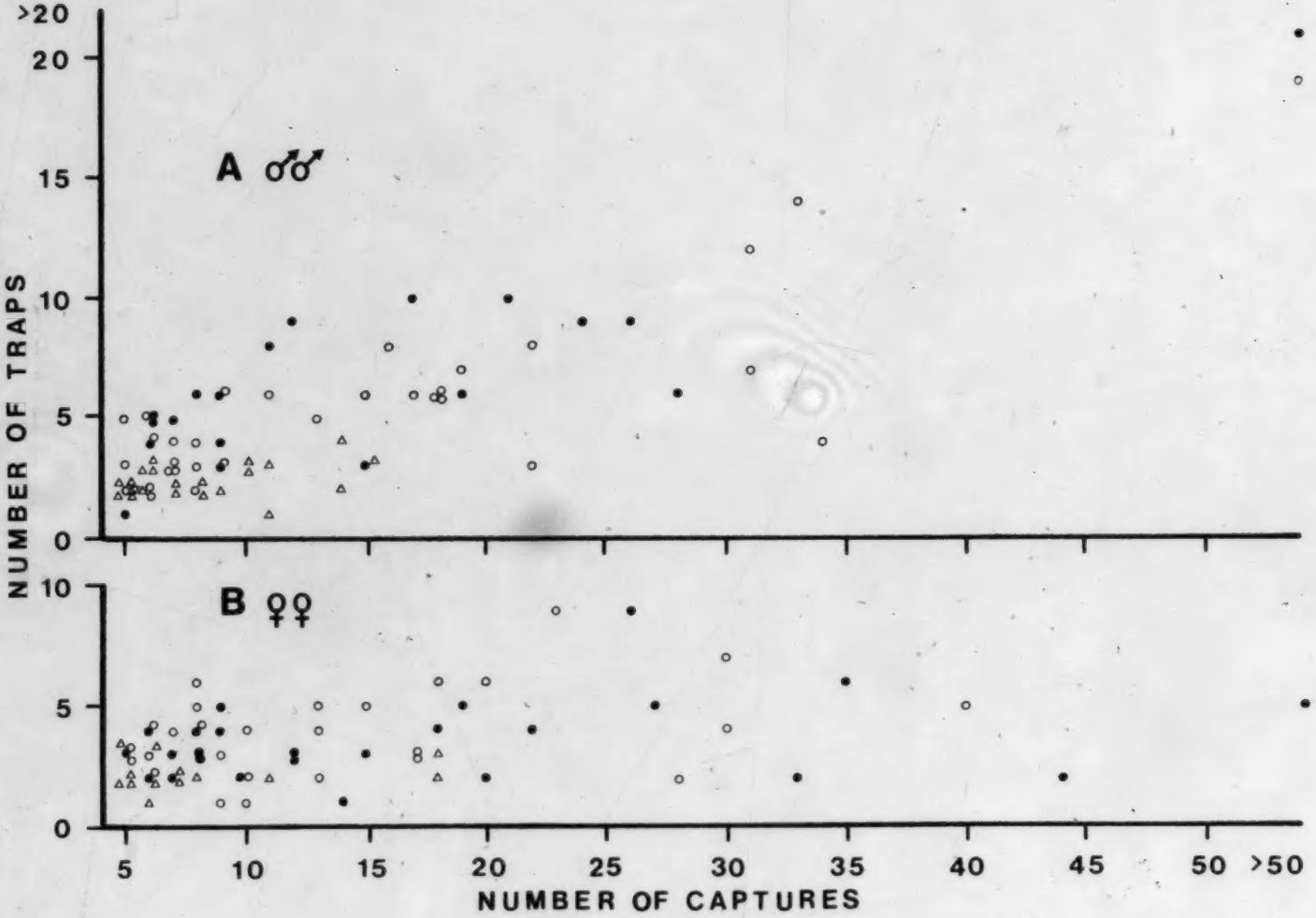
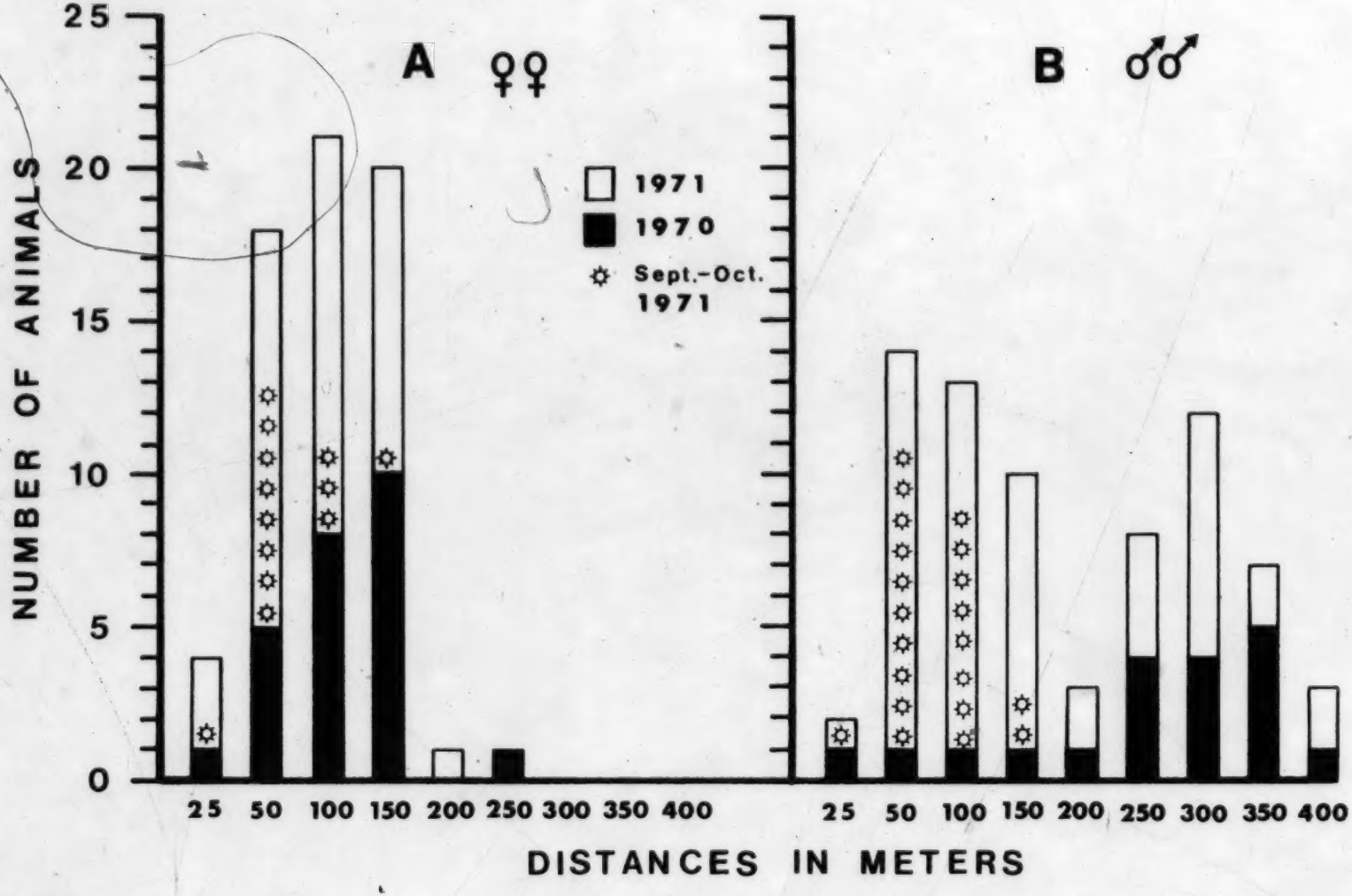

>20
20
15
10
5
0
A ♂♂
B ♀♀
NUMBER OF TRAPS
10
5
0
5
10
15
20
25
30
35
40
45
50
>50
NUMBER OF CAPTURES

Figure 11. Observed Range Lengths (ORL) of female (A) and male (B) *C. gapperi* during the trapping seasons of 1970 and 1971.


A ♀♀
B ♂♂
1971
1970
Sept.-Oct. 1971
NUMBER OF ANIMALS
0
5
10
15
20
25
25 50 100 150 200 250 300 350 400
25 50 100 150 200 250 300 350 400
DISTANCES IN METERS

main advantage is that fewer captures are necessary to determine ORL than to calculate range area (Stickel 1954). Observed range lengths were calculated for each individual trapped five or more times for the entire trapping seasons of 1970 and 1971 to get some idea of the total range covered by the voles, and at 2-week intervals during the trapping seasons to see if any seasonal variation occurred.

The female curve is unimodal in 1970, 1971 (spring-summer and fall), and the two years combined (Fig 11 A). Essentially all (97%) of the females had ORL's that were less than 151 m. Of the two females that had ORL's that exceeded 151 m the longer of these (201-250 m) belonged to a female that was captured near the end of the 1970 season (August) and the shorter (151-200 m) to a female captured in the spring of 1971. Most of the fall-captured females had ranges between 26-50 m.

The male curve is unimodal for 1970 with 79% of the animals having ranges exceeding 150 m (Fig 11 B). One male had a measured range of 400 m, but its true range may have been larger since it was bounded by one of the plot borders. Another male, with a measured ORL of 300 m, was also trapped approximately 3 trap intervals (150 m) beyond the western border of the plot. All of the first litter males of the season, six in number, had ORL's greater than 200 m.

The male curve is bimodal for 1971 and for the two years combined. Fall captured animals (40% of the total 1971 sample) contributed 60% of the short ranges (6-150 m), while overwintered animals contributed 17% of the short ranges. Of the longer ranges, 56% of the animals were overwintered males, while the rest were young of the year.

Males and females behaved quite differently, especially in 1970, with essentially no females exceeding range lengths of 150 m, while the

majority of male ranges were greater than 150 m. In 1970, all of the male young of the year had ranges greater then 200 m, while in 1971, the numbers were evenly divided (excluding the fall sample) with 50 % having long and 50% having short ranges.

Mean ORL's were calculated at 2 - week intervals for both years combined since sample sizes for each year taken separately were too small. Mean female ORL's (Fig 12) never exceeded 120 m and never dropped lower than 84 m, which was the value for the last trapping period in the fall. Fluctuatuons between these two values occurred, but they were not significant ($p<0.05$, Duncan's Multiple Range Test).

Male mean ORL's were unimodal (Fig 13), with midsummer values being significantly longer ($p<0.05$, Duncan's Multiple Range Test; Table 7) than early spring and late fall values.

Mean Intercapture Distance (MID)

Average distances moved between successive capture sites can be used as an index of extent of range. No adjustment was made to remove bias caused by using animals captured frequently. Means were calculated by combining the distances moved between captures within one complete plot rota, and dividing the combined value by the number of captures.

In 1970, males started at about one intertrap distance (Fig 14). As the season progressed, the MID increased to 2, and then to more than 3 intertrap distances. Females levelled off at 0.5 intertrap distances and never exceeded 1 intertrap distance.

In 1971, the pattern was similar for females. Males started the same as in 1970, but peaked at just over 2 intertrap distances. When breeding stopped in September-October, both males and females were moving about half an intertrap distance between captures.

Figure 12. Observed Range Length (ORL) for female C. gapperi by 2-week intervals, for 1970 and 1971 combined. Each 2-week period ends with the morning trap check and begins with the evening trap check on the dates shown. Horizontal lines are means; boxes show 95% confidence intervals; and vertical lines indicate ranges. Sample sizes in parentheses.

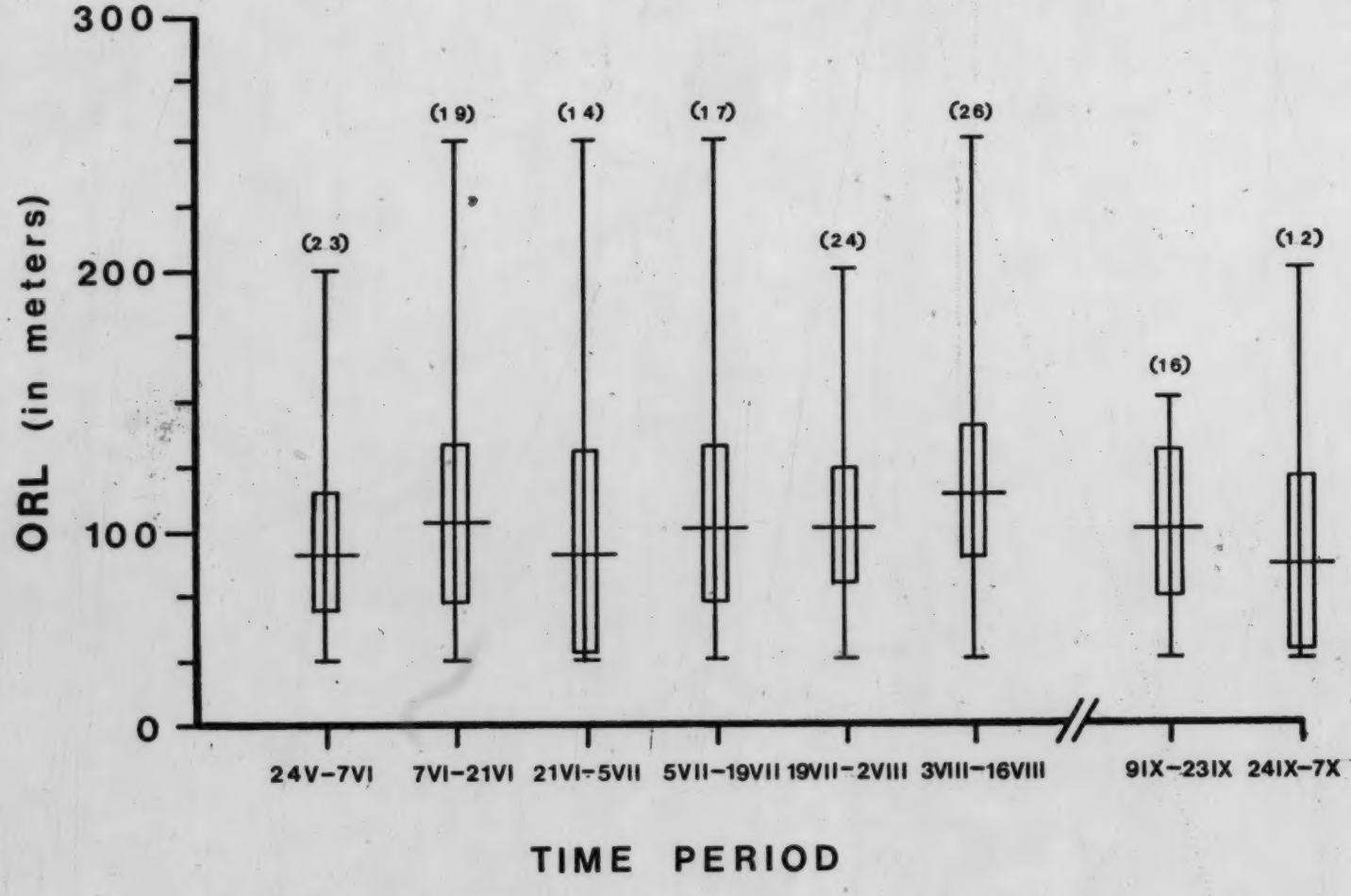

300
200
100
0
ORL (in meters)
(23)
(19)
(14)
(17)
(24)
(26)
(16)
(12)
24V-7VI
7VI-21VI
21VI-5VII
5VII-19VII
19VII-2VIII
3VIII-16VIII
9IX-23IX
24IX-7X
TIME PERIOD

Figure 13. Observed Range Length (ORL) for male C. gapperi taken at 2-week intervals, for 1970 and 1971 combined. Each 2-week period ends with the morning trap check and begins with the evening trap check on the dates shown. Horizontal lines are means; boxes show 95% confidence intervals; and vertical lines indicate ranges. Sample sizes in parentheses.

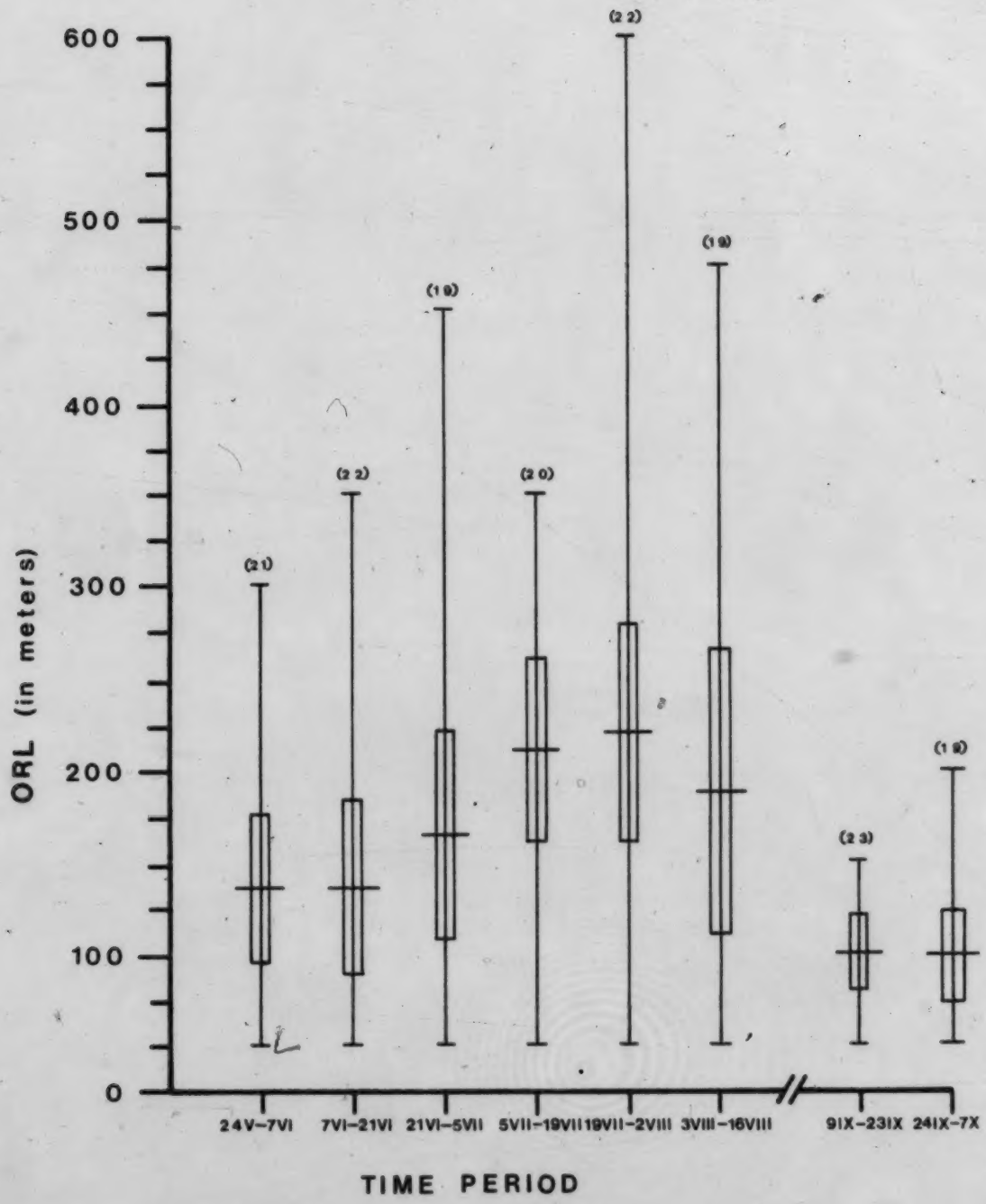
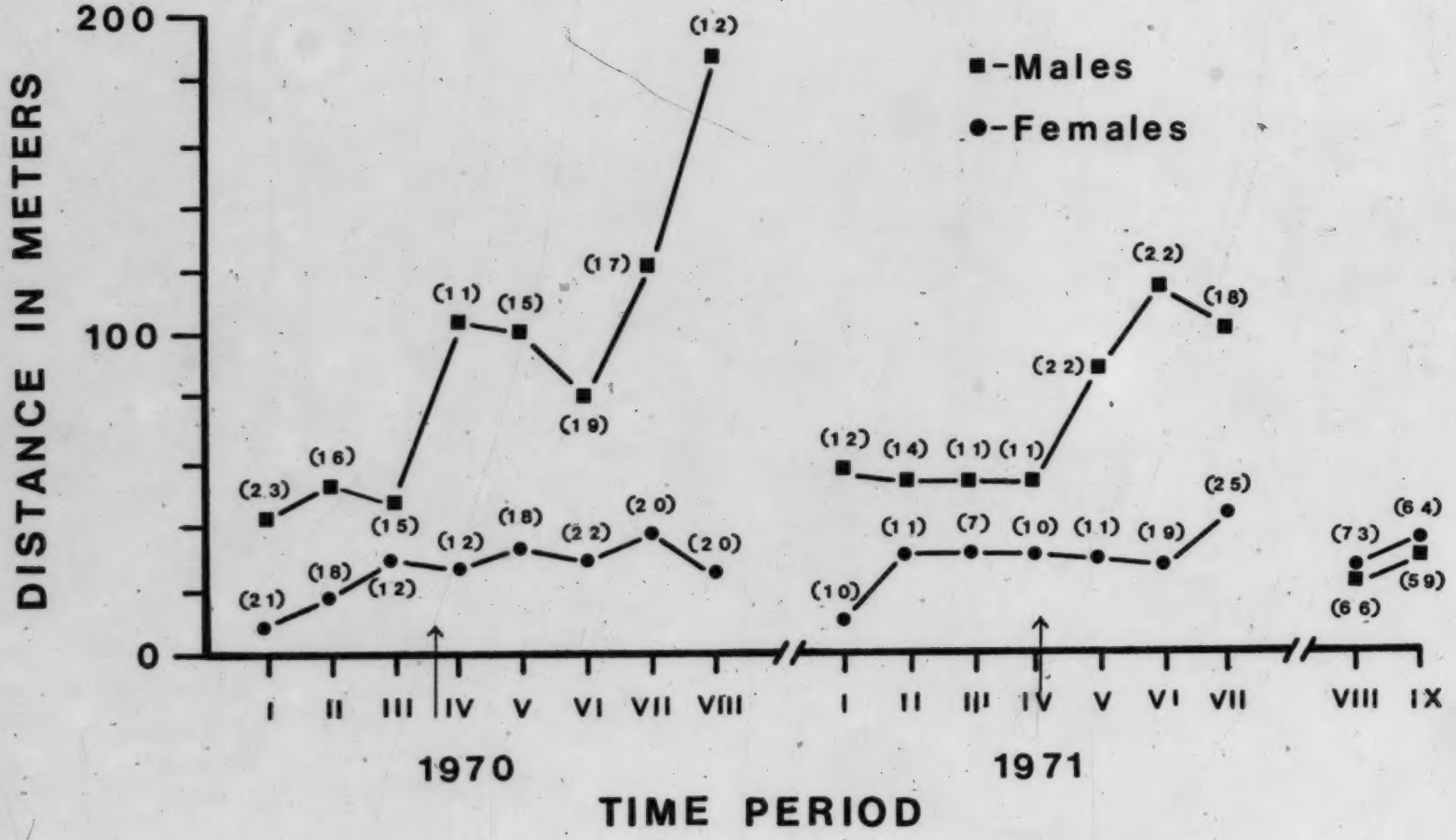

600
500
400
300
200
100
0
ORL (in meters)
(21)
(22)
(19)
(20)
(22)
(19)
(23)
(19)
24V–7VI
7VI–21VI
21VI–5VII
5VII–19VII
19VII–2VIII
3VIII–16VIII
9IX–23IX
24IX–7X
TIME PERIOD

Table 7. Significance of differences in mean Observed Range Lengths for male C. gapperi shown in Fig 13 (Duncan's Multiple Range Test; $p<0.05$).

24 IX-7 X	9 IX-23 IX	24 V-7 VI	7 VI-21 VI	21 VI-5 VII	3 VIII-16 VIII	5 VII-19 VII	19 VII-2 VIII
———							
		———	———	———			
					———	———	———

Figure 14. Mean Intercapture Distances (MID) by 2-week intervals. Numbers in parentheses indicate total number of each sex captured on the plot during each period. Arrows indicate approximate time of first appearance of young.


200
100
0
DISTANCE IN METERS
■-Males
●-Females
(12)
(11)
(15)
(17)
(19)
(23)
(16)
(15)
(21)
(18)
(12)
(12)
(18)
(22)
(20)
(20)
(22)
(22)
(18)
(12)
(14)
(11)
(11)
(10)
(11)
(7)
(10)
(11)
(19)
(25)
(64)
(73)
(59)
(66)
I II III IV V VI VII VIII
1970
I II III IV V VI VII VIII IX
1971
TIME PERIOD

In both years, increase in MID for males coincided with appearance of young, possibly because emergence of young may increase competition for traps, or because the young, in establishing a "known area", may be moving a great deal.

Both time period VI in 1970 and time period VII in 1971 indicated a drop in MID, which may be related to breeding. However, this drop occurred nearly two weeks later in 1971 than 1970 and instead of the MID increase observed in 1970, the trend in 1971 appeared to be the decrease of MID to half the intertrap distance, below even the lowest spring levels.

The MID's may be related to vole population density on the plot. Doubling of numbers of males in 1971 produced an increase in MID, while decreasing numbers in 1970 also produced an increase in MID, which however, was almost 1/3 greater than the increase observed in 1971. For the most part, fewer males on the plot prompted greater MID's but other factors may also be involved.

Minimum Polygon

Home range areas were plotted and calculated for each of the 3 periods (May-August 1970, May-August 1971, and September-October 1971) using the Minimum Polygon method. In order that data on all animals captured more than 5 times could be used, animals captured at only one trap point were given a home range area of 36 m^2. This was derived by using the radius of the circle centered on the marking stake within which traps were set (3 m) as half the side of a square having the stake at its geometric center. Where two or three traps in a straight line or two diagonally positioned traps were utilized, the area was taken as a rectangular corridor joining all the traps utilized, and having a width equal to the diameter of the circle within which traps were set (6 m).

Using this method of area calculation, the mean female range in 1970 was 2178.6 m^2 (Fig 15 A), while in the May-August period of 1971 it was 2391.3 m^2 (Fig 15 B). In both years, females never exceeded a home range area of 10,000 m^2.

Mean male range was 11,810.7 m^2 in 1970 (Fig 15 A) and 7317,8 m^2 in the May-August period of 1971 (Fig 15 B). More males had ranges which exceeded 10,000 m^2 in 1970 than 1971. In both years the largest range exceeded 28,000 m^2.

Fall captured females in 1971 had a mean area of 640.4 m^2 while fall captured males had a mean home range of 874.7 m^2.

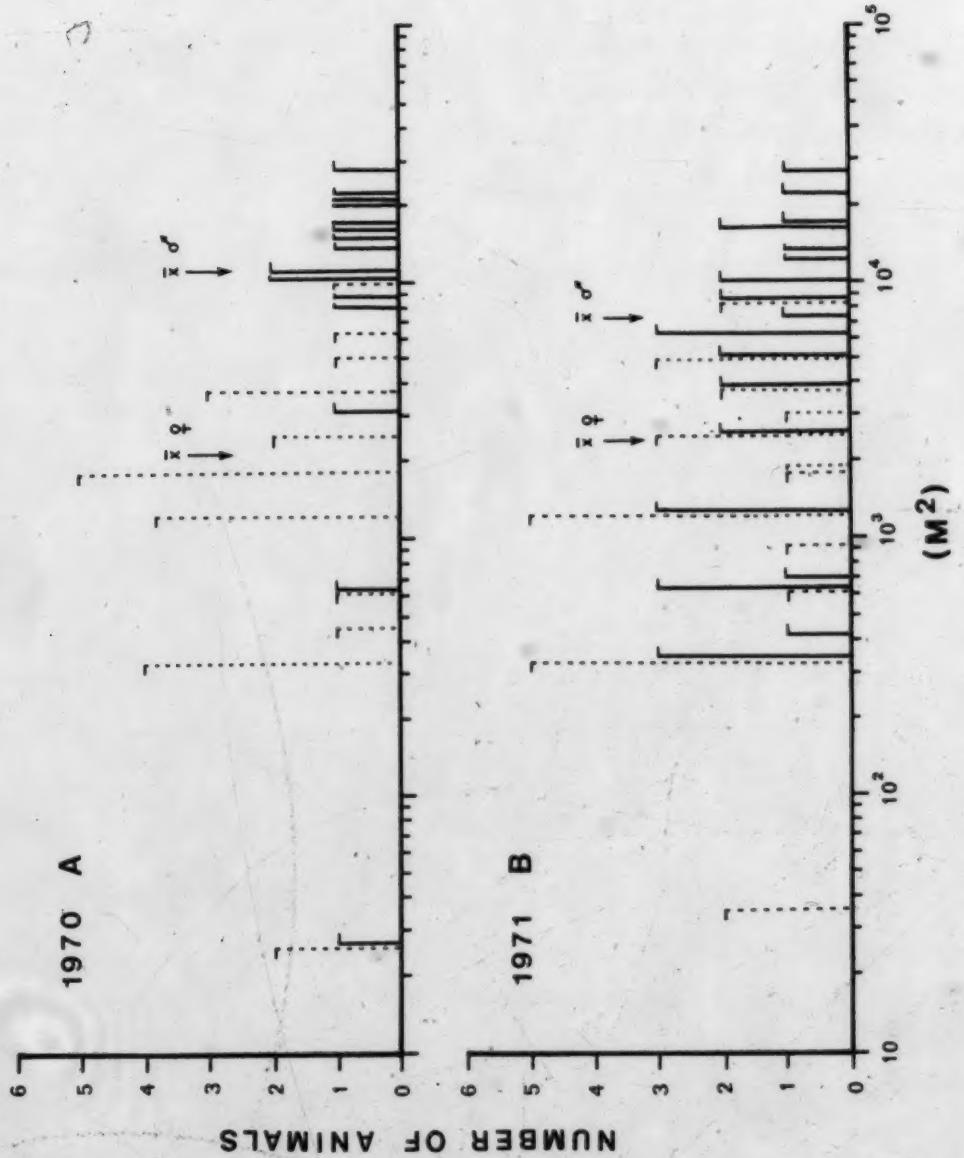
Exclusive Boundary Strip

Using this method, which is based on the assumption that animals range at least half way to the next capture site, a boundary strip equal in width to half the distance between traps is set off around the minimum area. For easier calculation, each trap point at which the animal is captured is considered as the center of the square whose sides equal the intertrap distance. These squares are then joined to each other so that they encompass a minimum amount of area. The area calculations were made for the entire season, and values, because of the methods employed in their calculation, are larger than the bare minimums expressed by the minimum polygon method.

The mean home range area for females remained basically the same in the spring-summer seasons of both years (Fig 16 A and B), being 9130.1 m^2 in 1971, and in 1970, 9003 m^2. Using this method, the largest female range area did not exceed 18,000 m^2 in 1971, and 23,000 m^2 in 1970.

Male ranges in 1970 and 1971 went to as high as 63,000 m^2 (Fig 16 A and B) and 40,000 m^2 respectively. The spring-summer mean in 1971 was 16,486.8 m^2, while in 1970, the mean was almost twice as large, at 28,814.5 m^2.

Figure 15. Home range area (in m^2) for male (solid line) and female (broken line) C. gapperi in the spring-summer trap seasons of 1970 (A) and 1971 (B) using the Minimum Polygon method of calculation. Seasonal means are indicated ($\bar{x}$).


1970 A
1971 B
NUMBER OF ANIMALS
(M²)
x̄ ♂
x̄ ♀
0
1
2
3
4
5
6
10
10²
10³
10⁴
10⁵

All of the September-October animals had small ranges (Fig 17 B) with a majority having range sizes of 5100 m^2 (i.e. 1 trap point). Some animals, both males and females, did, however, have a home range area greater than 10,000 m^2 during that time period. The mean ranges, however, were small and essentially the same in both sexes, with the mean value for fall females being 5933.6 m^2 and for males, 6382.8 m^2.

Seasonal Shifts and Multiple Trap Utilization

Females: Over intervals of two weeks, in 1970, female ranges usually formed two or three point configurations throughout the season (Fig 18). First and second litter females (for which ranges could be drawn) tended to be caught in a larger number of traps than did the overwintered females, thus giving the impression that they had a larger range. Not much apparent range disintegration occurred at the end of the trapping season. Although the trap-revealed ranges shifted and sizes fluctuated, animals could always be found in the same general area.

Two animals exhibited large movements in the spring (#23 and #26), one (#23) eventually establishing a home range on the plot. This spring mobility (also reflected by ORL increases, Fig 13) did not manifest itself at the end of the trapping season, and was due possibly to unsettledness resulting from breeding.

Home ranges overlapped only occasionally, and multiple use of a trap point by two females occurred only nine times during the season (Table 8). (I defined multiple use as capture of 2 or more animals at one trap site during a trap check.)

In 1971, ranges were initially larger than in 1970, but animal numbers were lower (Fig 19). As in 1970, ranges became larger as the season progressed and variations in areas and shifts in ranges occurred. At about the

Figure 16. Home range area (in m^2) for male (solid line) and female (broken line) C. gapperi in the spring-summer seasons of 1970 (A) and 1971 (B) using the Exclusive Boundary Strip method of calculation. Seasonal means are indicated ($\bar{X}$).

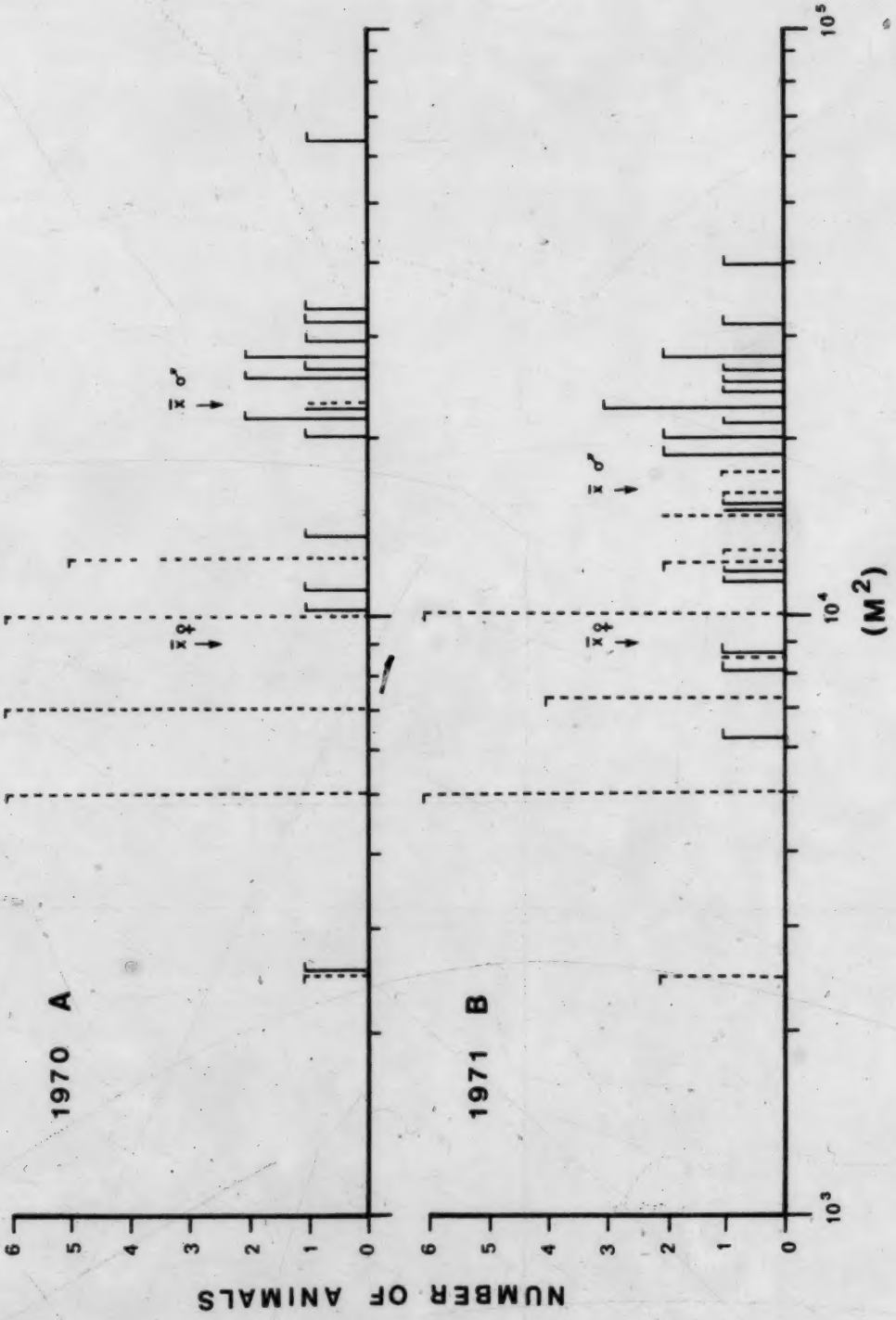

1970 A
1971 B
NUMBER OF ANIMALS
(M²)
x̄ ♂
x̄ ♀
0
1
2
3
4
5
6
10³
10⁴
10⁵

Figure 17. Home range area (in m^2) for male (solid line) and female (broken line) C. gapperi in September-October of 1971, using the Minimum Polygon (A) and Exclusive Boundary Strip (B) methods of calculation. Means are indicated ($\bar{x}$).

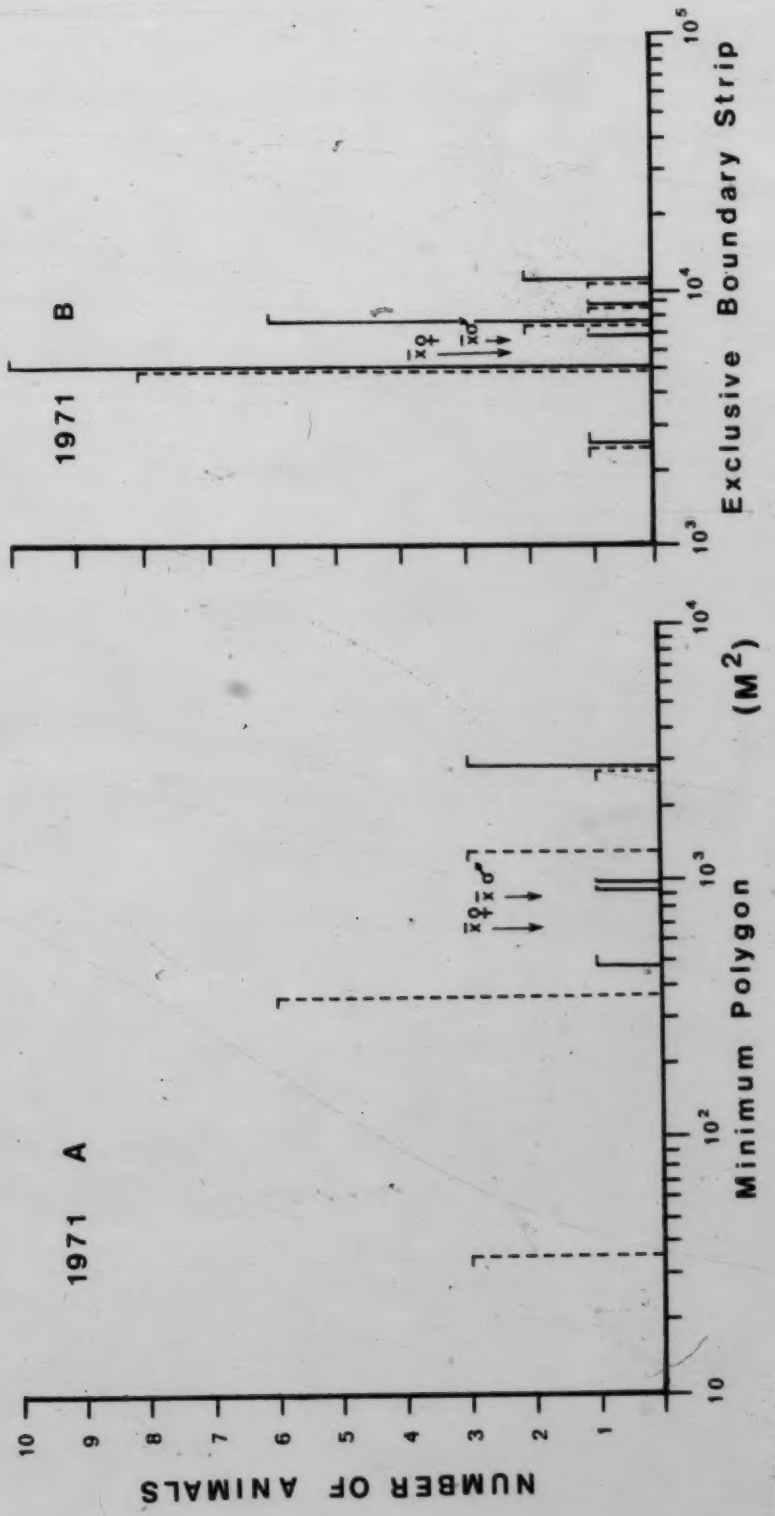
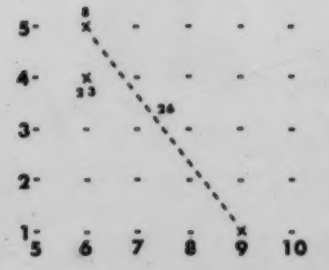

1971 A
1971 B
NUMBER OF ANIMALS
Minimum Polygon (M²)
Exclusive Boundary Strip
10
10²
10³
10⁴
10⁵
1
2
3
4
5
6
7
8
9
10

Figure 18. Selected female C. gapperi home ranges to indicate the following throughout the trapping periods of 1970:
(1) long movements at outset of the trapping season #26 and #23
(2) range changes or shifts throughout the season - in size and location, #23 and #8
(3) overlap of range, #88 and #8
(4) increase in range of young of the year, #76 and #77

I



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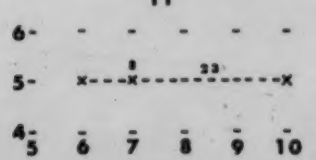
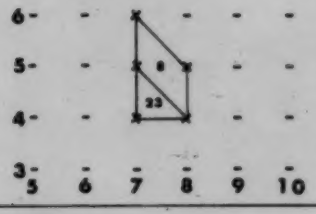


III

IV



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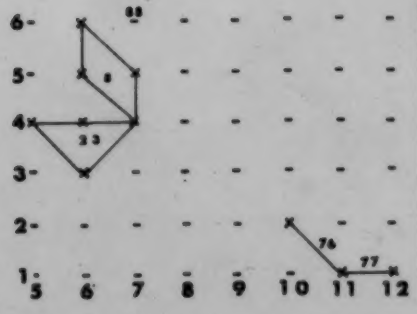

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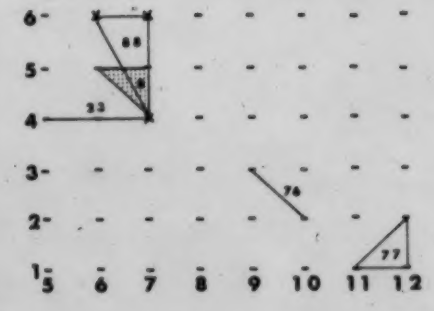
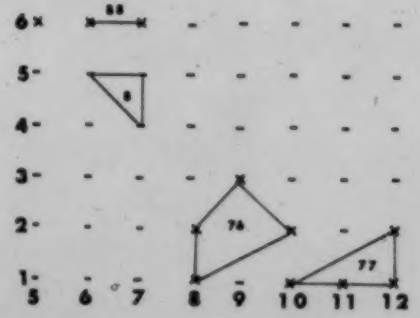
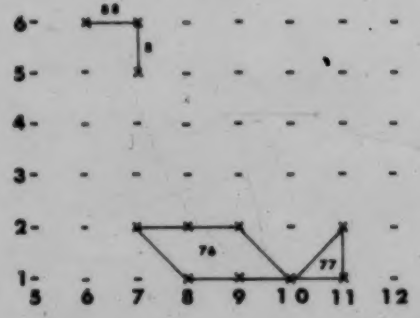


VII



VIII



time of emergence of the first litter, ranges generally decreased in size, with new animals being captured at only one or two points. This trend continued until period V, when even established overwintered females had reduced their area of concentration to one or two points. Later in August, however, trap-revealed ranges began to take shape, and increase in size. In September, when numbers of females had tripled, most were one point captures but a few three point and two point straight line ranges still existed. This trend continued until trapping ended in October.

Only two multiple female captures occurred during the spring-summer season of 1971 (Table 8). These increased to 15 multiple captures in the fall, however, numbers of animals present had also increased.

Males: In 1970 trap-revealed home ranges began initially quite small in comparison to the size they attained later in the season (Fig 20). From the time of emergence of the first litter, they continued to increase in size, overlap, and shift to encompass other areas as the season progressed. There was almost no difference between trap-revealed ranges of adults or young of the year. Many movements of up to 300 m occurred in both age classes. Range areas often comprised a corridor of utilized traps around a core of untouched ones, especially when ranges were large, and occasionally ranges appeared to be two separate areas not joined by a corridor. At the end of period VII the revealed ranges grew smaller and ended either as two point (straight lines) or one point captures in period VIII.

Only five instances of multiple use of trap sites occurred although in one instance three males were captured at one site at one trap check.

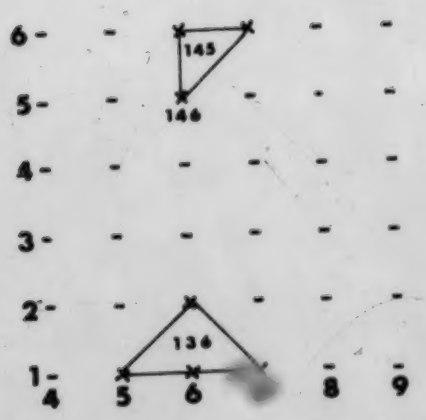
Fewer three point areas were initially evident in 1971 than 1970, although linear ranges occupied by males in 1971 often exceeded 300 m (Fig 21). The ranges continued to increase and during the season were large,

Table 8. Number of times different combinations of animals were caught in the three traps at any trapping point, during any one trap check, in the summers of 1970 and 1971, and the fall of 1971.

		Combinations						
		♂♂	♀♀	♂♀	♀♀♂	♂♂♀	♀♀♀	♂♂♂
May-August	1970	4	9	44	1	4	0	1
May-August	1971	16	2	44	1	4	0	0
September-October	1971	15	15	47	2	8	0	0
TOTAL		35	26	135	4	16	0	1

Figure 19. Selected female C. gapperi ranges (#136, #145, #146) to indicate the following throughout the trapping season of 1971:
(1) period III - decrease in range size
(2) period V - further decrease to 1 point areas; appearance of young animals
(3) period VII - plot inundated with animals, some 3 point ranges are evident.

I



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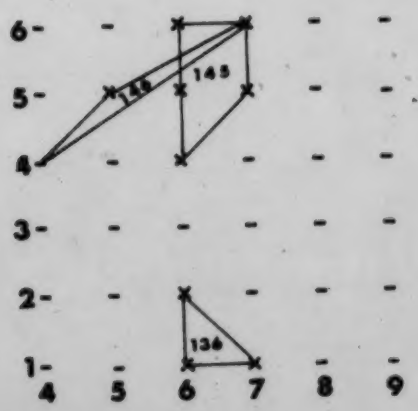

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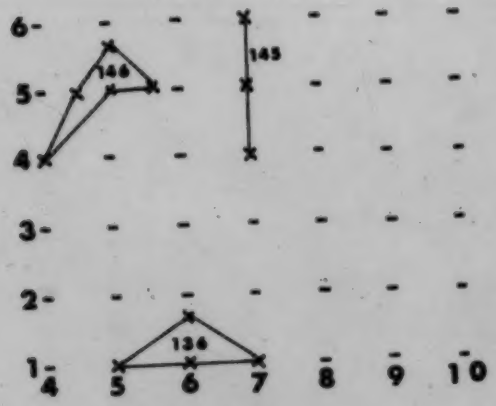

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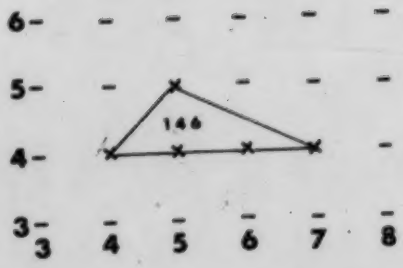
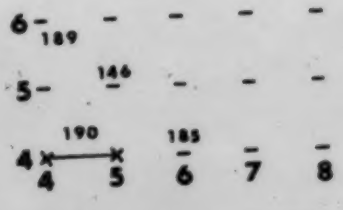
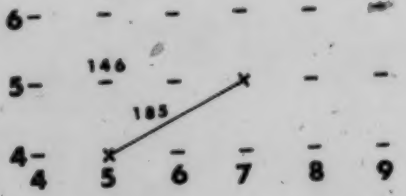


V



VI



VII

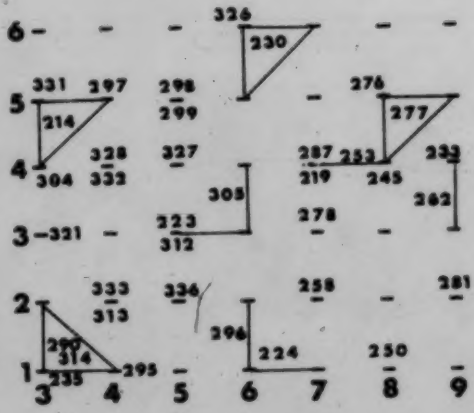
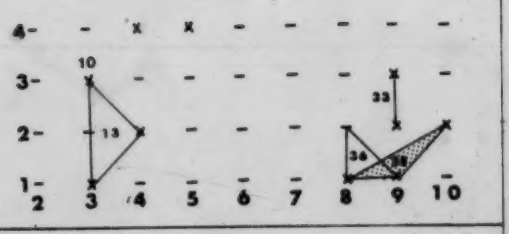


Figure 20. Selected male C. gapperi ranges to indicate the following as the season (1970) progresses:
(1) increase of range, range shift, overlap, and eventual disappearance, (#36, #13, #50)
(2) initial capture, disappearance, return and subsequent disappearance, (#21)
(3) ranges of young of the year (#92, #97)
(4) return in time period VIII to single point captures

I



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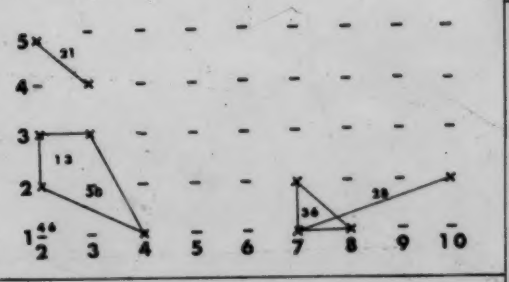
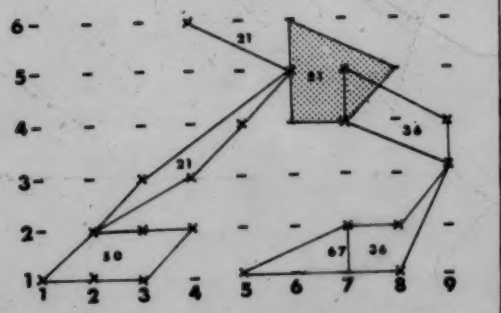
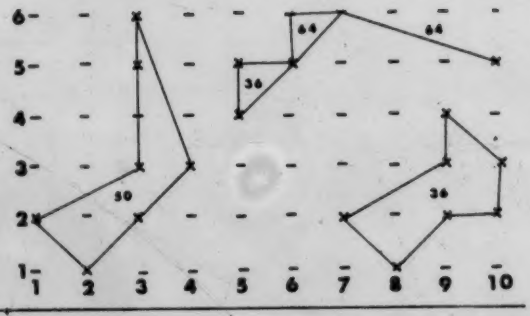


II

IV



V



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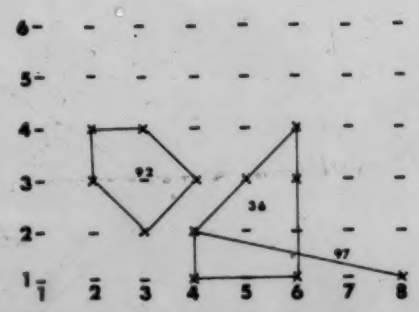

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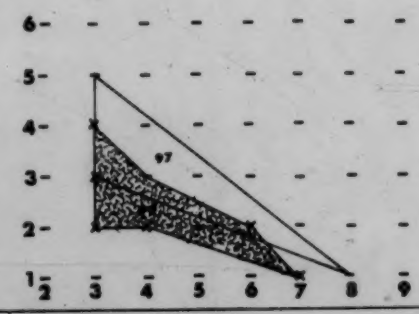
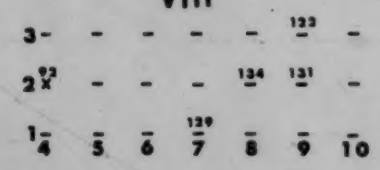


VIII



overlapped and shifted in areas they covered, getting smaller at the end of the season. These smaller fall ranges did not break up entirely as did the period VIII ranges in 1970, although numbers of animals greatly exceeded numbers present on the plot in 1970.

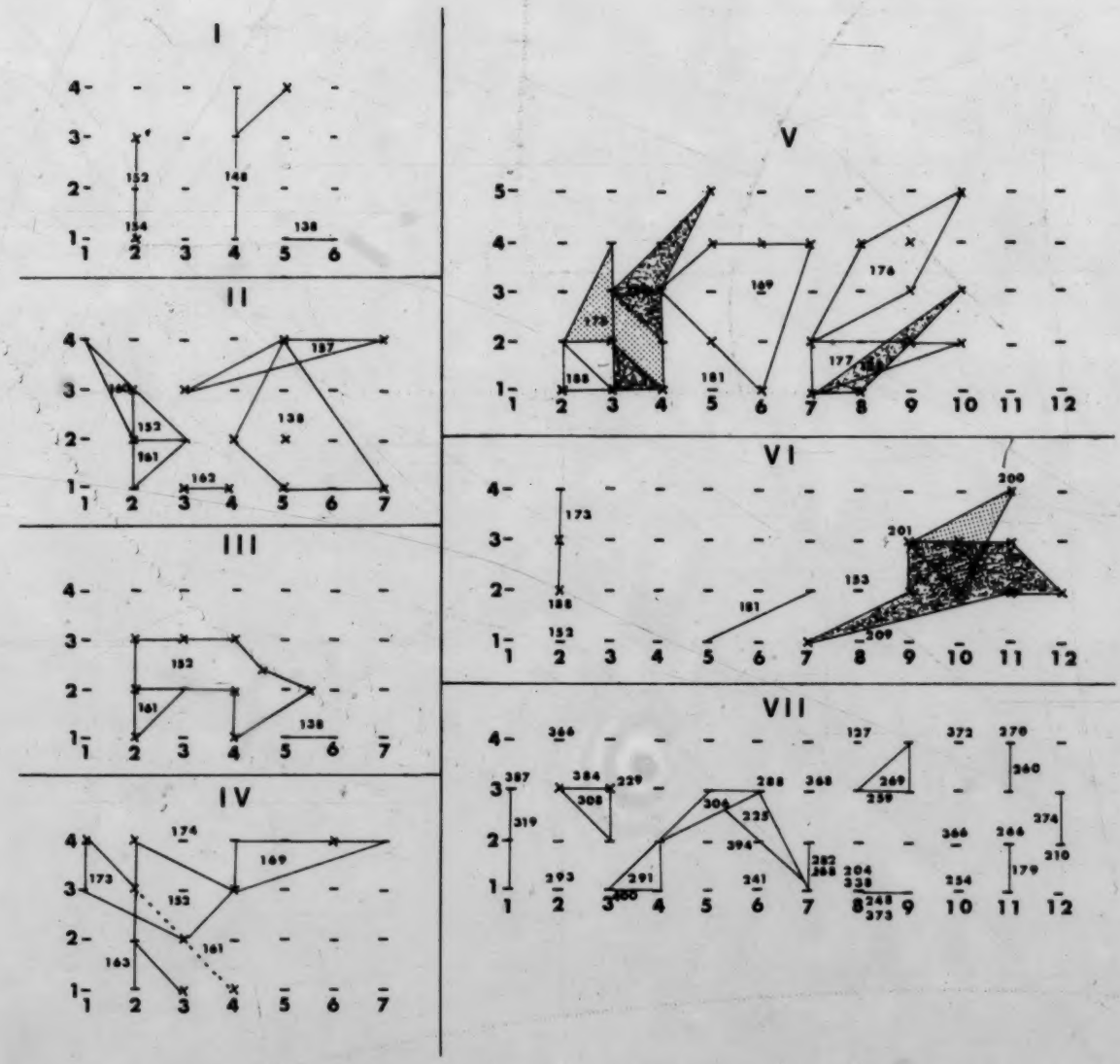
Four times as many males were multiply captured at one trap site in the spring-summer season of 1971 than the same period in 1970, again though numbers were lower (Table 8). Numbers of multiple captures per trap site in the fall season of 1971 equalled numbers captured in the spring-summer season of 1971.

Male - female associations are to be expected, and multiple use of a trap site by a male and female occurred more frequently than same sex multiple use, with values being the same for the spring-summer season of both years. Both sex multiple trap site use in the fall season of 1971 exceeded the value for the spring-summer season but number of animals was also greatly increased (Table 8).

Frequency of multiple utilization of a given trap site by animals of the same sex (Table 8, columns 2 and 4 compared with 1 and 2) suggests that males are more tolerant of each other than are females. Also, tolerance of females for each other increases in the fall, after breeding is terminated. If this is so, they may occupy the same area or actually share nests in winter for heat conservation.

In 1970 and 1971, two litters were born in traps and were subsequently removed by the female (presumably). On two occasions in 1970 and on 4 occasions in 1971 during the spring-summer season a male and a female were both found in one trap.

Figure 21. Selected male C. gapperi ranges to indicate range differences throughout the season (1971);
(1) straight line ranges in time period I
(2) increases, shifts and overlap of ranges in time period II and III
(3) ranges of young of the year with shifts (#173, #169), overlap of ranges of young and adults, decline of adult ranges (#152),
(4) presence of small (3 point) ranges in the fall (time period VII.


I
II
III
IV
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VI
VII

DISCUSSION

Studies comparing trapping to other methods of determining home range parameters, including isotope marking, tracking using sand or smoked paper, fecal dyes and bits of yarn, mechanical-electrical sensing and recording, direct observation, and auto photographic recording have indicated that trap revealed home ranges have several disadvantages. Justice (1961) enumerated the three most important disadvantages as 1) trap inhibition - the trap impedes the animal's movements; 2) a strong positive or negative learning experience may result; and 3) trap fatigue from frequent trapping causes loss of animal life. The Capture-Mark-release (CMR) method, however, may offer a basic estimate of the amount of area that an animal does cover, providing that other factors are taken into consideration. In particular, emphasis must be placed on assessing an adequate plot size and the best trap spacing for the most reliable estimate of home range size.

Nikitina (1965) stated that optimum size for a plot for the study of home range in the red vole (C. rutilus) was 5.8 ha, however, plot size was dependent upon relief and vegetation, season of work, mobility of animals in that particular area, and the character of their settlement. Also, she noted that the most efficient trap spacing for C. glareolus was between 10 and 20 m. At 50 m animals were captured only a few times and usually at one or two points. Hayne (1950), in a study of M. pennsylvanicus, also noted that increased trap spacing increased the apparent area of the home range. This was also demonstrated by Mohr (1947) and Stickel (1954).

In this study, the 50 m grid on the 14 ha plot was too large to accurately define the home ranges of females. Males, however, ranged

extensively on the plot as well as beyond its confines, thus only a few male ranges were entirely delineated. The larger grid in this study may have been more accurate for male ranges because of the type or distribution of vegetation (density or a paucity of certain plant species in certain areas of the plot; plot A was subjectively termed inferior), and because of the density of the animals themselves. Kikkawa (1964) suggested that more accurate measurement of home range is possible if trapping procedure involves a combination of grid sizes, thus including animals with small ranges. Perhaps if the 50 m grid had been used to get general location of the animals, a smaller grid could then have been adopted to further delineate a more accurate home range size. This would, however have necessitated the use of many traps or some other recording technique. A moving grid, allowing smaller trap spacing was attempted in this study, but probably the duration was not long enough and the area chosen for intensive trapping was not suitable.

Dependence of range size on distance between traps is obtained only if traps are located in one place for a fairly long period of time (Nikitina 1965). Relocation of traps is necessary so that animals do not become accustomed to them, and use them as refuges and feeding places. Constant utilization of the same traps and the exclusion of others would tend to decrease the range size because only known and favored traps would be frequented. If this is true, the large ranges demonstrated in this study might be caused in part by the fact that traps were not relocated for the entire trapping season and could, perhaps, have been easier to find. The traps, however, were closed alternate weeks, so that the animals could not always depend on the availability of a particular trap as a refuge. Some animals, particularly females, were recaptured repeatedly

at one or two trap points. This could be an indication that certain animals depended on some of the traps or knew of their location and frequented them. There is some consolation, in a case like this, in that these animals were not actively seeking out traps. This may also be an indication that trap spacing was too large. Nonetheless, the trap-revealed ranges may have been partly determined by the presence of traps.

Nikitina (1965) stated that within one week animals became used to a trap in forested areas, while Hamar and Sutova-Hamar (1968) suggested that range determinations should be made during an interval not exceeding 20 - 30 days. Since in this study traps were closed alternate weeks, just as the animal found the trap and began to frequent it, the trap would be closed, hence becoming unavailable to the animal. This could deter the animal from returning to that particular point; however, closed traps occasionally had feces and tracks (muddy smudges) on them indicating that they were being visited and explored although they were not open.

Chitty (1937) found that mice were caught in one line or two parallel lines of traps, especially when traps of a grid system were set far apart. He explained that placing traps in lines may have caused animals to follow lines and alter the shape of the range from one governed by natural distribution to one influenced by regular spacing of traps. But linearity may be duplicated by setting traps more than one range width apart (Hayne (1950). Then animals are caught only by those traps on or near the long axis of their real ranges. In some studies, however, home ranges have been found to be linear due either to habitat preference of the species being studied (Zejda 1971), or to the method of analysis (Mazurkiewicz 1969, 1971, Mohr 1965, Godfrey 1954). In this study, although the traps were widely spaced, females, with their smaller ranges still managed to

travel to at least three different trap points, these points only rarely being in a straight line. Males too, did not shift to a linear type of range, so the trap spacing was not so great as to make them adopt exclusively linear ranges. However, in some cases in both males and females, linear movents were observed, especially in the spring for females, and throughout the season in males. Spring linear movements were attributed to increased activity and establishment of a more commonly utilized area of the known range in females. In males, linear movements away from the more commonly utilized range were attributed to the greater mobility of microtine males as reported in the literature (Tanton 1969, Smirnov 1967, Van Vleck 1968, and others).

Burt (1943) excluded "sallies" from the usual range area and referred to them as being exploratory in nature. Kendeigh (1944) noted that if homing behavior is based on previous knowledge of the area, then animals must have larger ranges than recorded in the literature. There are indications that subadults may travel the entire extent of a study area, while adults, who are more or less established in their home ranges, cover smaller portions of the same area (Stickel 1954). Although recorded home range areas are comparatively small, records of extreme movements have been made, which take the form of a long trip with a subsequent return to the home range (Storer, Evans and Palmer 1944, Sheppe 1967, Iverson and Turner 1972). Though these movements are usually infrequently noted in any particular trapping period, they may be important in orientation and may explain the apparent familiarity with large range areas disclosed in various homing studies (Chitty 1937, Stickel 1954). These movements may also represent a natural tendency for exploration necessary for invasion of depopulated areas, gene pool mixing, or extension of species

ranges (Stickel 1954). There are indications that individuals making long distance movements have lower probabilities of capture in live-traps than other animals (Faust et al. 1971) thus necessitating greater sampling efforts or use of other techniques to compensate for biases inherent in live-trapping. Sheppe (1967), utilizing both tracking and trapping techniques, noted that traps may have some effect on behavior of mice (P. leucopus) by increasing their activity. He also suggested that occasional movements outside established home ranges were probably caused by physiological changes produced by confinement in traps. Because the mouse's tendency to explore and re-explore its surroundings is thwarted when the animal is in the trap, the increased activity after the animal is released may be compensatory (Sheppe 1966). Because of this after-trapping effect, ranges may be artificially enlarged and temporary changes of movement should be expected and could interfere with detailed studies of range utilization.

Several animals made exploratory trips in this study, but such trips were only obvious for females and only when the range map for the whole season was examined. Males did not appear to be restricted to a home base, and if trips were exploratory in nature, they were hard to separate from normal movements, again, unless range maps for the entire season were analysed. This suggests that two techniques are employed in gaining familiarity with the surroundings. Perhaps males, since they do not need to center on a home in one position, can establish the large ranges suggested by Kendeigh (1944). Females, restricted by presence of young in a permanent or semi-permanent home nest can only afford to make exploratory trips i.e. "sallies". Sheppe's (1966) "after-trapping" effect could be possible in several cases in this study, most notably, in the

case where a released male moved a distance of three trap points in 20-30 minutes. This is only conjecture.

If increased home range overlapping is accompanied by increased number of contacts then degree of overlap tolerated should give some indication of territoriality or exclusiveness in home range (Koshkina 1965, Getz 1961). Harvey and Barbour (1965) noted overlap in male ranges of M. ochrogaster, and Tanaka (1972) could find no evidence of territoriality in M. montebelli since both male and female ranges overlapped considerably. Friesen (1972), however, in a pen study noted that a territory was necessary for C. gapperi females to successfully raise a litter. He suggested, on the basis of other criteria, that territorial areas could be quite small and perhaps included only that area immediately surrounding the nest site. Getz (1961) found that, although overlap occurred in Microtus, percentage of animals having unshared portions of their home ranges showed no relationship with density, thus indicating a degree of territoriality. He also noted that the actual defended area was quite small, about 7 m in diameter, although range areas were from 200 to 800 m^2. Getz (1961) also used multiple captures as an indication (he stressed the use of this term) in determining territoriality on the assumption that animals of the same sex would not be trapped together if their ranges were exclusive.

Although no sweeping conclusions regarding territoriality could be deduced from this study, in most cases ranges overlapped, suggesting lack of territoriality. Also, multiple captures of same sex animals at one trap point in this study, when males are considered, increased when numbers of males decreased (from spring-summer 1970 to spring-summer 1971), while multiple captures of females decreased when total numbers of females decreased during this same time period. Perhaps, however, as Friesen (1972)

mentioned, females are territorial but defend only a very small portion of their range.

Young females in this study usually first appeared near an established range of an adult female. In a few cases the trap-revealed ranges of young animals overlapped the range of an adult. Perhaps, as Frank (1957) and Getz (1961) noted in Microtus, and Howard (1949) noted in P. m. bairdi young females remain in the immediate vicinity of the mother's range. Young males may leave the vicinity, although they may not move too far away, as in M. agrestis (Godfrey 1953). This could not be determined, because males were very mobile, and only a few juveniles of either sex were initially captured or established range areas near already present adult females.

Estimation of home range size on the basis of prolonged trapping has been criticised because over a long period of time, e.g. a month, the animal may repeatedly change its range (Dunaway and Kaye 1961, Kikkawa 1964, Ambrose 1969, Tanaka 1972, Mazurkiewicz 1971). With area use patterns changing as environmental, behavioral, and physiological conditions change, constant revelation of new points could be an indication of changes in distribution of the animals in the area, i.e. changes in the home range (Adamczyk et al. 1966). In this study, shifts in revealed ranges were noted during the entire trapping season, particularly in the case of males, although females tended to shift their range to a lesser extent. These shifts of range from one area to another, along with nomadic behavior, may only indicate, particularly in males, that several homesites are being utilized (Blair 1951). In some species the adult female moves, leaving the old area occupied by the young (Burt 1940). If the adult female shifted her range area slightly to accommodate another

individual, the few obvious adult female - young male or female range overlaps and shifts that occurred in this study might be explained. Mazurkiewicz's (1971) finding, that male ranges shifted more than female ranges, was substantiated by this study, because males normally moved about more.

Variations in home range size from year to year in a given area are one way that animals adapt to environmental conditions, including density (Stickel 1954). Buckner (1957) found that differences in range size in two different areas in C. gapperi might be a reflection of habitat utilization, since all foraging took place on the ground on one plot, while foraging excursions into trees on the other plot limited the horizontal component of range. Blair (1940) stated that smaller food supply in sparsely vegetated areas resulted in larger home ranges than in areas in which vegetation was more abundant. Getz (1961) found that reduction in range area was probably more the result of unfavorable environmental conditions than abundance of vegetation, with increase in home range size in spring resulting from more moderate environmental conditions that permitted foraging (in M. pennsylvanicus). In this study, initial increase in range was synchronous with onset of breeding and arrival of spring. My study plot, however, comprised a mosaic of favorable and less favorable habitats (Fig 1), but I am unable to say whether home range size was related to habitat type in the way that either Blair (1940) or Getz (1961) suggested. Most male ranges could not be assigned to a specific community type because males ranged widely over two or more contiguous units. Although females more often restricted their activity to a single community type, there were no marked differences in the indices of home range size. There were, however, more female home ranges in the spruce and aspen areas than in the park-like jack pine and open juniper types.

Several factors are supposed to exert a strong influence on the trappability of the population itself - factors such as the individual's chance of being captured, the degree of interest in traps being exhibited by the population as a whole (Kikkawa 1964), and the social structure of the population. Home range dynamics have also been related to behavioral interactions among the individuals of the species (Naza et al. 1973).

The most trappable individuals of a population are assumed to have the largest living areas, occupying phytosociological habitats preferred by rodents, and entering traps earliest after they have been opened (Andrzejewski et al. 1967). The younger the individual, the lower its trappability (Gliwicz 1970) due to its smaller living area (Ryszkowski 1962) and because it is driven away from traps by older individuals, particularly during periods of extensive competition (Kikkawa 1964), and it approaches traps late and finds them occupied (Tanaka 1963).

The oldest individuals are known to exhibit differences in trappability according to sex (Ryszkowski 1962, Kikkawa 1964, Gliwicz 1970). Among individuals of other cohorts, age and rate of maturation, not sex, are the determining factors (Gliwicz 1970). First litter females should, as the season progresses, have a higher trappability than males of the same age group or of both males and females of younger cohorts (Gliwicz 1970).

However, each trapping period has a slightly different population density (different trap to individual ratios) and different climatic and phenological conditions, all of which may have an effect on trappability.

Throughout the literature, in those species in which the male is polygamous, males tend to have larger ranges and wander more than do females presumably because the latter have to care for young, although frequency of recapture may be the same in both sexes (Van Vleck 1968).

Such was the case in this study. Contrary to wide-spread opinion (eg. Gliwicz 1970) that males are more subject to being trapped, both sexes were recaptured with equal frequency, although throughout the season male ranges tended to exceed female ranges. Increases in male home ranges were noted when trapping was initiated in spring, probably because of the onset of breeding activities, i.e. active search for mates as well as milder environmental conditions. Ranges of young males of the year, or at least the first litter were as large as those of adult males. Average trap-revealed distances moved between captures increased dramatically as the season progressed possibly because of the movement of animals across and off the plot (emigration).

Females, too, increased range size in spring but actual area of range stabilized after the initial increase. Observed range lengths fluctuated but this is probably an artifact of the method of analysis. Average distances moved between captures remained the same once ranges had been established.

Gliwicz (1970) observed that differences in trappability of individuals of different sexes and ages disappeared in fall, and Mazurkiewicz (1970) noted that home range size tended to become uniform then. Both authors suggested that change in social structure after termination of breeding was a likely cause, and that individuals exhibited a tendency to clumped dispersion before the winter period. Reduction of summer aggression has been reported in C. gapperi (Friesen 1972, Watts 1970), which should increase winter survival by reducing energy expenditure.

Home ranges in this study tended to disintegrate in the fall in both sexes, although no aggregation or clumping (Beer 1961, Formozov 1946) was evident. This disintegration of home range may be due to trapping

mechanics. If the ranges had merely become smaller, and if clumping or at least concentration of many small ranges in some areas had been occurring, it would not have been noted on the large grid. However, some animals were extremely mobile, so perhaps constant turnover of animals did not allow for established range areas. If the trapping season had been extended, perhaps clumping or aggregation would have been detected prior to the first snowfall or after the hiemal threshold had been attained.

Decrease in size of male and female ranges to a fraction of their summer size in the late fall may be correlated with increased population density and greater apparent mobility of the entire population, or the breaking down of social, sexual and chronological barriers (Gliwicz 1970) which gives all animals an equal chance to enter traps. If increased mobility is induced by activation of the reproductive organs (Beer and Meyer 1951, Howard 1960), there should be no fall upheaval, because the fall population consists of a few old animals that have ceased to breed and many young ones that did not attain puberty in the summer of their birth. This general fall upheaval might facilitate mixing of the gene pool, and it could confer an advantage on any animal surviving the winter, because, during the period of great mobility the individuals could become familiar with a large area which could stand them in good stead when establishing a home range in the following spring. Perhaps these animals are the ones that become the "Dominants" mentioned by Andrzejewski et al. (1967).

In the fall of 1971, increase of numbers (doubling of spring-summer numbers) occurred along with great mobility and disintegration of ranges. These animals may have been second and third litter animals that had not

made their appearance until the fall upheaval for the following reasons: 1) young were not captured until forced into competition with adults due to changed parental behavior in driving them away form the nests (Gliwicz 1970); 2) after leaving the nest, young have a tendency for clumped dispersion which limits chances of encountering a vacant trap, because existing traps are presumably occupied by older or sexually mature adults (Gliwicz 1970) (although in this study three traps were provided at each trap point). As fall approached, social, sexual and chronological barriers broke down, and all animals had relatively equal chances to enter traps, thus offering one explanation for the large numbers noted in the fall of 1971. These animals may have been off the plot avoiding the traps, or they may have moved from more or less favorable areas surrounding the plot. Chitty and Phipps (1966) noted a large increase in numbers of young C. glareolus in July and suspected, with uncertainty, that they were immigrants. Animals were also added to their study area in the non-breeding season. Here again, their origin was obscure.

The observed shifts in sex ratio in fall 1971 and spring 1972 are perplexing. In the fall of 1971, live-trapping results indicated that numbers of males in the population had begun to decline, although not significantly. The reduced numbers may have been due to a trapping artifact. Mature females are, during the spring-summer periods, presumably occupied by caring for litters. They may have avoided traps or may not have been able to move around quite as much because of their litters. In the fall, however, as litters matured, they were able to move around more freely and thus were able to find more traps. The fall snap-trapping results were in favor of the males, although again not significantly. However, the spring excess of males as revealed by snap-trapping, especially

if plot A alone is considered, was nearly large enough for statistical significance. Tendency to snap- and live-trap more males than females has been observed in a number of studies (Townsend 1935, Tanton 1969, Smirnov 1967) and is believed to be due to greater wandering tendency and greater activity in males. Since plot A had fewer animals than plot B in the fall of 1971, perhaps plot B was being chosen as the area of clumping or aggregation if such occurred. When spring snap-trapping was carried out in 1972, plot A may still have had fewer animals than plot B, but more males may have been caught because of their greater activity. Perhaps plot B was the wintering area and provided plot A, through emigres, with its summer complement of breeding animals.

Hayne (1949), Stickel (1954), Sanderson (1966), Mohr and Stumpf (1966) have all enumerated and made comparative studies of various methods of home range calculations and concluded that they all have, in certain instances various advantages and disadvantages. Studies on methods of calculation are still being made with the ultimate goal of determining the most accurate method of calculation. Even with all the improvements however, various assumptions have to be made regarding either shape of range, accuracy of capture, the animal's behavior, or any of a score of factors aslo influencing range size.

In this study, average ORL's for the entire season did not differ much from the average ORL taken at 2-week intervals for either males or females (Table 9). The ORL values were much larger than those obtained for M. pennsylvanicus (Ambrose 1969), M. agrestis (Godfrey 1954), and M. montibelli (Tanaka 1972) (Table 10). In each of these studies, however, grid and plot sizes were smaller than in this study and obviously, different species were studied.

Mean Intercapture Distance (MID) for males in this study was more than twice the distance for females who seldom moved farther than the inter-trap distance (50.29 m).

The minimum polygon method of area determination gave smaller values in this study than exclusive boundary strip values. This is reasonable, however, because of the methods employed in calculation (Stickel 1954). When compared with published winter values (0. 1 ha) obtained by Beer (1961) for C. gapperi (Table 10), fall values in this study (0.09 ha for males and 0.07 ha for females), as well as being more similar than spring-summer values for both sexes, are slightly, though not significantly, smaller. Spring-summer range areas for both sexes in 1970 and 1971, calculated by the minimum polygon method, (1.18 ha for males and 0.22 ha for females in 1970; 0.73 ha for males and 0.24 ha for females in 1971) are smaller than those obtained in a fall to spring study of C. gapperi by Iverson and Turner (1972) with 1970 values for males in this study more closely resembling values obtained by Iverson and Turner (1972) for females. They assumed elliptical ranges, however, and areas were calculated by the method of Jenrich and Turner (1969).

When home range areas were determined using the exclusive boundary strip method, the 1970 and 1971 values for males obtained in this study (2.3 ha and 1.6 ha respectively) were larger than Iverson and Turner's (1972) value although the range areas obtained for females in this study, which were the same in both years (0.90 ha), were still smaller than their 1.23 ha value. Fall values, using the exclusive boundary strip method, yeilded almost equal areas for both males and females, and all values were larger than those obtained for other species (Table 10). Metzgar and Sheldon's (1974) method of calculation gave range areas closely approximating those obtained using the minimum polygon method.

Table 9. Comparison of mean home range lengths and areas of C. gapperi resulting from different methods of calculation. Data are those obtained in this study.

	SIZE OF RANGE		METHOD OF CALCULATION
	♂	♀	
Entire season	200 m	106 m	Observed Range Length (ORL)
2 week periods	152 m	98.6 m	Observed Range Length (ORL)
2 week periods	82 m	30 m	Mean Intercapture Distance (MID)
1970 Spring-Summer	1.18 ha	.22 ha	Minimum Polygon
1971 Spring-Summer	.73 ha	.24 ha	Minimum Polygon
Fall	.09 ha	.07 ha	Minimum Polygon
1970 Spring-Summer	2.28 ha	.90 ha	Exclusive Boundary Strip
1971 Spring-Summer	1.65 ha	.91 ha	Exclusive Boundary Strip
Fall	.64 ha	.59 ha	Exclusive Boundary Strip

Metzgar and Sheldon's (1974) method of calculation gave range areas closely approximating those obtained using the minimum polygon method.

Table 10. Comparative mean home range lengths and areas in several Microtine rodents as reported in the literature, with range areas and plot sizes converted to hectares. (Compare with Table 9.)

Authors	Animal	Size of Range ♂	Size of Range ♀	Method of Calculation	Grid Size	Plot Size
Getz, 1961	M. pennsylvanicus	* .02–.08 ha		Exclusive Boundary Strip	15 m	3.6 ha
Hayne, 1950	M. pennsylvanicus	.42 ha	.06–.08 ha	Exclusive Boundary Strip	60 ft	4.85 ha
Hayne, 1950	M. pennsylvanicus	.27 ha	.18 ha	Exclusive Boundary Strip	120 ft	4.85 ha
Brown, 1956	M. agrestis	1.0 ha	.05 ha			
Harvey & Barbour 1965	M. ochrogaster	* .09 ha		Minimum Polygon, Isotope Marking		
Brown, 1956	C. glareolus	* .16 ha				
Kikkawa, 1964	C. glareolus	.22 ha	.11 ha	Manville Method	11 m	1.75 ha
Zejda & Pelikan, 1969	C. glareolus	.08 ha	.07 ha	Inclusive Boundary Strip	15 m	3.8 ha
Bujalska, 1970	C. glareolus		.06–.09 ha	Wierzbowska's (1972) Method	15 m	4.0 ha
Mazurkiewicz, 1971	C. glareolus	* .30 ha		Wierzbowska, 1972	15 m	4.0 ha
Beer, 1961	C. gapperi	* .10 ha		Minimum Polygon	50 ft	5.25 ha
Iverson & Turner, 1972	C. gapperi	1.83 ha	1.23 ha	Elliptical (Jenrich & Turner, 1969)	20 m	3.24 ha
Ambrose, 1969	M. pennsylvanicus	.04 ha	.02 ha	Isotope marking		
Ambrose, 1969	M. pennsylvanicus	27.4 m	21.7 m	Observed Range Length		
Godfrey, 1954	M. agrestis	* .02 ha		Isotope Marking		
Godfrey, 1954	M. agrestis	*26.4±1.51 m		Observed Range Length	10 m	1.0 ha
Tanaka, 1972	M. montebelli	.04 ha	.02 ha	Ellipse (ORL x ORW)		
Tanaka, 1972	M. montebelli	28.2±1.57 m	19.9±1.04 m	Observed Range Length	10 m	1.0 ha

* average for both sexes taken together

CONCLUSIONS

1. Values for home ranges as determined by the various methods in this were higher than most recorded in the literature for other Microtines, and with the exception of values obtained by Iverson and Turner (1972), they were several times larger than those recorded in the literature for C. gapperi.
2. Ranges overlapped considerably in both males and females, which suggests lack of territoriality. However, the trap grid may not have been sensitive enough, because of its large size, to detect actual avoidance. Multiple use of one trap area per trap check suggests that males were more tolerant of each other than females, and that tolerance of females for each other increased in the fall. In a few cases, trap-revealed ranges of adult females were overlapped by ranges of young of either sex, although it could not be determined whether or not the young animal was the offspring of the adult. Amount of overlap appeared to increase as the season progressed and hence as the numbers of animals on the plot increased (indicating that young animals were settling on the plot, although not in entirely unoccupied areas).
3. Compared with females, males showed a tendency to use more traps as numbers of captures increased, and hence, covered much larger range areas and moved considerably longer distances between successive captures, although both sexes were captured with equal frequency.
4. Seasonal differences in ORL were observed for males, but not for females. Soon after trapping was initiated in the spring, male ranges began to increase in size, reaching a peak in July. Average range size decreased in August, and by September and October had returned to the low level of early spring. Females showed a similar trend, but none of the

observed differences were statistically significant. MID also tended to increase seasonally, apparently not being affected by numbers on the plot. Values peaked in August of 1970 when numbers on the plot were low, and in June of 1971 when numbers on the plot were higher, although the 1971 peak was not as great as the 1970 peak. Low fall values may be seasonal or they may be the result of larger numbers.

5. As vole population density increased, as the season progressed, parts of the plot which were not previously utilized became inhabited by new animals, or ranges of animals already present shifted to incorporate a part not previously utilized by the animal. However, home ranges did not appear to become smaller as population numbers increased.
6. Ranges of overwintered animals were larger than those of animals captured in the fall, but smaller fall range sizes could possibly be attributed to break down of social, sexual, and chronological barriers if such existed. Young attaining sexual maturity early in summer had ranges as large as, or in some cases larger than, those of over wintered adults. Those attaining sexual maturity later had smaller ranges.

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